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The Development
of the
Cartilaginous Skull and of the Branchial and Hypoglossal
Musculature in Necturus.

Inaugural-Dissertation

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Ernst Haeckel

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The Development of the Cartilaginous Skull and of the Branchial and Hypoglossal Musculature in Necturus.

Introduction.

It is now several years since KASTSCHENKO ('88) first called attention to the fact that many cells of the neural crest in the head of the Selachian embryo do not take part in the formation of the nervous system, but give rise to reticular mesoderm, or mesenchyma. It was, however, already known to those interested in the early development of the nervous system, that the anterior part of the neural crest is not represented in corresponding ganglia. In 1878 MARSHALL showed that the neural crest extends forwards to the level of the optic outgrowth, consequently beyond the region in which the ciliary and trigeminal ganglia are found. v. WIJHE ('82) also described the anterior division of the neural crest in the Selachii as extending from the anterior part of the hind-brain even beyond the optic vesicles, thus occupying the whole width of the mid-brain. v. WIJHE tells us that this anterior part of the neural crest gradually vanishes from before backwards, adding that he cannot say with certainty what becomes of it.

KASTSCHENKO, however, definitely states that the cells thus lost from the neural crest neither degenerate, nor take part in the formation of nervous tissues, but add themselves directly to the mesenchyma, a tissue which, in the opinion of KASTSCHENKO, is

nothing other than the sum of the embryonic cells which have been left unused in the formation of epithelial organs (*loc. cit.*). We have here ground for a seemingly sharp distinction between structures formed from epithelia which may be traced directly to one or other of the primitive germ-layers, and structures of mesenchymal origin, in the formation of which any or all of the germ-layers may participate. This distinction, however, is not as definite as it at first might seem. Cells of the mesenchyma, primarily derived from epithelial layers, may again secondarily associate themselves in the formation of epithelia. Thus, the wall of the »anterior« head-cavity in the Selachii is formed from scattered cells, i. e. mesenchyma, of endodermic origin, yet, at the stage of its highest development, the wall of this head-cavity is perfectly epithelial in structure, differing apparently in no wise from the wall of the neighboring mandibular cavity, which traces its origin directly to the primitive mesodermic germ-layer, and ultimately gives rise to the mandibular muscles.

Moreover, the homologue of an organ derived in one Vertebrate from epithelial tissues, may, in another Vertebrate, be derived from the mesenchyma. Thus, the eye-muscles which develop in the epithelial walls of the praemandibular, mandibular, and third head-cavities in the Selachii, are formed in the Amphibia in the mesenchymal tissue median to the optic vesicles. These instances serve to show that the distinction between epithelial and mesenchymal tissues is indefinite, and that the division of the mesoderm on the basis of this distinction lacks wide morphological significance, although most conveniently descriptive of actual histological conditions. Doubt which attaches to the origin of one part of the middle-layer, does not leave the other part altogether unaffected, but rather brings into question the morphological value of the whole.

Is there in the Vertebrata a median germ-layer, whose cells have a common origin, and which gives rise to definite systems of organs? V. KÖLLIKER ('84, page 201) answers this question by ably defending the view that it is no longer possible to associate each germ-layer exclusively with one or more tissues, but that each layer is capable of giving rise to all of the principal tissues.

Observed processes of growth, however, seem to warrant the assumption that, in the Vertebrata, at the time of gastrulation, the cells of the inner layer have been so far differentiated that they are no longer capable of producing nervous tissues, and that the cells of the outer layer are no longer able to fulfil the digestive functions

of the organism. Where the two primitive germ-layers pass into one another, along the margin of the blastopore, or in the line of its morphological equivalent, lies the area of doubt, coextensive with the mesoderm which is here proliferated. Not only is the degree of specialization which has taken place in the cells of the mesoderm open to question on the basis of the ectodermic or endodermic affinities of the tissues they subsequently produce, the very origin of the cells is doubtful, for in the highest Vertebrates the cells of the middle layer arise from the ectoderm; in the lowest Vertebrates — unless *Amphioxus* be, as LWOFF ('94) claims, an exception — the mesoderm is derived from the endoderm, while in intermediate forms both of the two primitive germ-layers contribute to its formation.

This difference of origin is explained by coenogenetic changes which, in separating the two primitive germ-layers, associate the band of cells destined to give rise to the mesoderm with one or other of the primitive layers according as the line of separation passes along the ectodermic or endodermic margin of the band. Thus, if the separation of the two germ-layers takes place along the endodermic margin of the band of cells from which the mesoderm arises, this tissue appears to be derived from the ectoderm, or from the endoderm when the conditions are reversed.

Although the explanation is simple, the complications produced by coenogenetic digressions from the plan of typical gastrulation, have led to the greatest divergence of opinion regarding the actual and theoretical, or phylogenetic, origin of the mesoderm, as amply testified in the critical reviews of MEHNERT ('91), and KEIBEL ('93).

When one turns from the question of the origin of the mesoderm to ask, what are the organs to which the middle layer gives rise? The answer is not less indefinite. The mesoderm gives rise to muscles. Yes, but v. KÖLLIKER ('84) tells us that the outer germ-layer possibly gives rise also to nonstriated muscle fibres in connection with glands of the skin, since, as first maintained by v. KÖLLIKER ('49), and afterwards confirmed by LEYDIG, and RANVIER, muscle cells are found between the secretory cells of the gland and its connective tissue covering. v. KÖLLIKER admits, however, that other interpretations regarding the origin of these muscle cells are possible. It may be said that there is no reason for assuming that the outer surface of the mesoderm is always bounded by connective tissue, or it may be held that these muscle fibres are formed by wandering

cells of mesodermic origin, and v. KÖLLIKER ('84) considers the question of their origin in any case enigmatical.

HEIDENHAIN ('93), however, calls attention to the fact that the muscle cells in question are connected, in the Amphibia, with the epidermis by intercellular strands of protoplasm similar to those found between the epidermis cells, and finds in this organic continuity evidence that the muscle cells belong genetically to the outer germ-layer. v. KÖLLIKER ('84) moreover, adds that the same difficulty occurs in connection with the endoderm, since here also smooth muscle fibres have been found immediately on the endodermal epithelium of the lung in the Mammalian embryo, as testified by STIEDA ('78) and himself ('79).

The vascular system is claimed for the mesoderm.

Yet GOETTE tells us that in the Amphibia ('75) and in *Petromyzon* ('90), the first blood cells come from the endoderm, and his observations have been confirmed by SCHWINK ('91). HOUSSAY ('93) also affirms that the endoderm takes part in the formation of the vascular system in *Axolotl*, while HOFFMANN ('93) even claims an endodermic origin for the vascular system in the *Selachii*¹. GOETTE is inclined to believe the endodermic origin of the blood the more primitive, while ZIEGLER ('92, page 28), regarding the mesoderm as the primitive source of vascular tissue, calls attention to the fact that the blood cells in the Amphibia arise in places, where, in the younger embryo, there was a continuous connection between mesoderm and endoderm, from which ZIEGLER concludes that it is »theoretisch denkbar« that in the course of phylogeny the place of origin of the blood was displaced from the mesoderm to the endoderm. In the Urodela and young Mammalia, the spleen is a source of red blood-corpuscles. The Mammalian spleen is of mesodermic origin, but according to MAURER ('90), the spleen of Amphibia is derived from the endoderm.

ZIEGLER adds that most zoologists assign to the endothelium of the blood vessels the same origin as to the blood corpuscles. The endothelium is therefore usually described as mesodermic, but GOETTE (loc. cit.) and SCHWINK (loc. cit.) derive the endothelium of the heart in the Amphibia and in *Petromyzon* from the endoderm, and

¹ My sections of *Acanthias* embryos convince me that HOFFMANN was unfortunate in the preservation of the material on which this statement is based.

RABL ('87) confirms the statement for the Amphibia, while RÜCKERT ('88) affirms that in the Selachii, individual cells migrate from the wall of the alimentary canal to take part in the formation of the heart and blood-vessels.

In *Necturus*, cells which form the endothelium of the heart also appear to arise from the endoderm. There are, however, mesodermic cells in the immediate neighbourhood, to which these endothelial cells might possibly be traced by one strongly convinced that the origin of the vascular system is, or ought to be, throughout mesodermic. However, the ventral blood-vessel (i. e. heart) immediately divides into two large vessels that run forwards and upwards to the dorsal aorta, through the mandibular arch. In *Necturus*, these mandibular aortae arise as spaces enclosed by thin protoplasmic extensions from cells still remaining in the wall of the alimentary canal (fig. 19, pl. XVIII). That these cells consequently are endodermic is not open to question. It is not even »theoretisch denkbar« that they have been displaced from the mesoderm at an earlier stage, for the axial mesoderm primarily extends in *Necturus* no farther than the transverse plane in which the chorda ends, or to the plane of the hyomandibular clefts. Anterior to this plane, the ectoderm rests directly on the endoderm with no intervening mesoderm. When the mesoderm finally extends forwards beyond the plane of the hyomandibular clefts, it does so as a distinct and sharply defined tissue, by no means continuous with the endoderm. Hence there can be no thought of an earlier fusion between the mesoderm and endoderm in the region in which the mandibular arteries arise. Moreover, the cells from which the mandibular arteries are formed, are not from the wall of the wide archenteron, but from the wall of the anteriorly closed tube of the alimentary canal.

In giving the grounds for believing the mesoderm to be the true source of the vascular system, ZIEGLER (loc. cit.) says: »In the Anura and in all Amniota the marrow of bones is concerned in the production of red blood corpuscles: no one will doubt that the marrow of bone belongs to the mesoderm and, indeed, to the mesenchyma.« Now, according to KASTSCHENKO (loc. cit.), the mesenchyma is in part ectodermic, and according to GORONOWITSCH ('92, page 456) just this ectodermic part of the mesenchyma contributes in the bird to the formation of bone. How then may we be sure that no cells of ectodermic origin take part in the formation of the vascular system?

I ask this question, not that I think the vascular system ectodermic, but merely to call attention to the fact that even the origin of blood corpuscles in the marrow of bone does not prove beyond all question their mesodermic origin.

It is probable that RABL ('94) and HARRISON ('94) were right in thinking inadequate methods responsible for a mistake, when KLAATSCH ('94, '95) derived the scleroblasts of Teleostei from the external ectoderm, nevertheless the origin of the skeleton is still open to question, since KASTSCHENKO (loc. cit.) believes mesenchymal tissues to be the product of cells contributed from all of the germ-layers, while GORONOWITSCH ('92) finds that that part of the mesenchyma which contains the lost cells of the neural crest gives rise to bone. Moreover, in a preliminary notice ('93) I have maintained that the branchial cartilages in *Necturus* arise from wandering ectodermic cells, while v. KUPFFER ('95) describes the branchial cartilages in *Petromyzon* as formed by cells of the deeper layers of the ectoderm in situ. The doubt which attaches to the origin of the mesoderm affects the chorda in like degree, since like the mesoderm, this axial structure, arising from the region where ectoderm and endoderm typically unite, seems in higher Vertebrates a product of the ectoderm, and of the endoderm in lower Vertebrates.

v. KÖLLIKER ('84) calls attention to the marked difference in the kinds of tissue derived from the outer germ-layer. First, there are two tissues so fundamentally different as nervous tissue and the outer skin, with which the epithelia bounding the cavities of the central nervous system might be compared. Further, the medullary plate gives rise to a peculiar supporting tissue which is certainly not widely different from real connective tissue, and which v. KÖLLIKER is inclined to place among the connective tissues.

I need merely mention the discussion regarding the ectodermic or mesodermic origin of the pronephric duct, as enough has been said to show that there is hardly an important system of mesodermic tissues — excepting only the reproductive glands — which is not in one or another Vertebrate, by one or another investigator, attributed, in whole or in part, to either the outer or the inner germ-layer, if not to both. It is therefore evident that in the term »mesoderm«, we have grouped together cells of widely different origin, and that we describe as »mesodermic tissues« many tissues which are in part at least derived from other germ-layers. If there be a middle germ-layer, with our present knowledge, it cannot be defined.

It is possible to explain the conflicting facts in accordance with the view advocated by v. KÖLLIKER (*loc. cit.*), and to maintain that the protoplasmic differentiation in embryonic tissues is so slight that any cell may, at the need of the organism, replace another. Thus the ultimate fate of any cell would depend chiefly on its position in relation to surrounding cells. Such a supposition makes early embryonic development the result of mechanical rather than chemical changes in the growing organism, and tends in the direction of the experimental work of WILSON, MORGAN, ROUX, and others, by whom it has been shown that cells separated in early cleavage stages may each develop into an entire organism, when under normal conditions, each such cell gives rise but to a definite part of the individual formed from the whole egg.

BARFURTH ('95, page 349) notes, however, in the report on Regeneration, that the experiments of DRIESCH ('95) on Echinoderm larvae lead him to conclude that the ectoderm is not capable of reproducing the lost cells from which the mesenchyma, and digestive tract are formed. BARFURTH's own experimental study of the regeneration of the germ-layers in the Amphibia lead to the same result as regards the independence and specialization of the germ-layers, which is further confirmed by MORGAN ('95). BARFURTH also cites the experiments of BARTH ('95) on the implantation of bone as tending to demonstrate the independence of the layers. We stand before the fact, BARFURTH says (page 374), that on the one hand the entoderm, if you choose, cannot replace the ectoderm in regenerative development, while on the other hand both layers in typical development may produce epithelia as well as glands, muscles, and other tissues, and the question consequently arises, whether, for example, a smooth muscle fibre derived from the mesenchyma is actually in every respect similar to the smooth muscle fibre produced by the ectoderm.

Although the mesoderm was once associated with the ectoderm as a source of nervous tissue, it is at present seldom, if ever, affirmed that the mesoderm takes part in the formation of nerves or ganglia, unless, with KASTSCHENKO (*loc. cit.*) and GORONOWITSCH ('92), we include in the mesoderm, i. e. mesenchyma, all wandering cells of whatever origin, that chance, even temporarily, to lose their epithelial connection.

The normal development of the peripheral nervous system in lower Vertebrates, with the attendant growth of nerve fibres from

scattered peripheral cells of ectodermic origin, as in the course of the ramus ophthalmicus profundus trigemini, or of the nerve trochlearis, is in itself a demonstration of the exclusive assumption of nervous functions by the cells of the ectoderm. The formation of nerve fibres from such scattered cells — mesenchymal cells, save for their ectodermic origin — has been described by V. KUPFFER in *Petromyzon* ('90, '91), by BEARD ('87, '88), FRORIEP ('91a) and myself ('91) in the *Selachii*, and by myself in *Necturus* ('96). It plainly shows that the wandering ectodermic (mesenchymal?) cell does not lose the ectodermic properties which distinguish it from neighboring cells of different origin.

Perhaps no more striking instance of the independence of the ectoderm, as well as of the potential equivalence of all ectodermic cells can be found than that furnished by the regeneration of the lens, after extirpation in the *Urodela*, from the marginal epithelium of the retina. This replacement of a highly modified, and essentially non-nervous structure, originally derived from the external ectoderm, by cells belonging genetically to the infolded ectoderm of the central nervous system is described by WOLFF ('94, '95) and confirmed by MÜLLER ('96).

Thus the phenomena of regeneration, as well as the normal development of ectodermic and endodermic tissues in the *Vertebrata*, speak strongly against the theory that each layer is capable of giving rise to all of the principal tissues. What we need is the explanation of the participation of more than one germ-layer in the formation of so-called mesodermic tissues, and of these tissues alone.

A theoretical explanation lies near at hand. It is possible to suppose that, in the developing egg at the blastula stage, the protoplasm at opposite poles becomes differentiated in the direction of ectodermic or endodermic properties mutually exclusive of one another. At the same time an equatorial band of cells is deprived of these strictly ectodermic or endodermic properties (which we imagine concentrated in the cells at the opposite poles of the egg), but retains certain properties of which the polar cells have been deprived (ex. reproductive properties). We may suppose that there remain, however, a group of properties (ex. muscular) potentially common to all of the cells of the egg should circumstances call for their development, although usually developed in the band of equatorial cells alone, which in the infolded gastrula represent the mesoderm. Perhaps the theory would correspond more closely with observed

facts of development, if it were further assumed that certain properties, usually developed in the equatorial cells (ex. skeletal) are potentially properties of the cells at the ectodermic pole of the egg, while excluded from the cells at the endodermic pole, and that other properties of the equatorial cells (ex. vascular) are potential properties of the cells of the endodermic pole, but not of the ectodermic.

Such a theory accounts for the inability of one germ-layer to replace another, since no two are in all respects potentially equivalent. It also seems to meet the conditions of actual development better than the long accepted view that each germ-layer differs absolutely from the others in the kind of tissue it can produce, or than the more recent theory that any tissue may arise from any germ-layer. The association of endodermic cells with the mesoderm in the formation of vascular tissue seems to me significant in consideration of the fact that in lower organisms circulatory functions belong to the digestive tract, and have been assumed by the mesoderm during the evolution of higher forms. A similar reason for the association of ectodermic cells with the mesoderm in the formation of supportive or protective tissues suggests itself, since of the two primitive germ-layers, it was doubtless the ectodermic which originally fulfilled these functions.

However, before any theory can be accepted as adequate, we need to know, as BARFURTH suggests, whether the smooth muscle fibre produced by the ectoderm is in every way similar to that derived from the mesenchyma; we need to know whether cells which leave their epithelial connection and wander into the mesenchyma lose or retain the primitive characteristics of the layers from which they are derived. In short, we need to know the origin and fate of all of the cellular elements of which the mesenchyma is composed.

The first effort to determine what becomes of the cells of the neural crest after they enter the mesenchyma came from GORONOWITSCH ('92) in a preliminary paper, entitled »Die axiale und die laterale Kopfmetamerie der Vogelembryonen. Die Rolle der sog. 'Ganglienleisten' im Aufbau der Nervenstämme«. In this paper GORONOWITSCH notes that the cells of the neural crest become scattered as they approach the dorsal part of the axial mesoderm, with which they soon absolutely identify themselves, so that the two kinds of cells cannot be distinguished (page 456). One can only say in general that the elements of the scattered neural crest group themselves in a region dorso-lateral to the axial mesoderm, from

which GORONOWITSCH concludes that the most extensively developed part of the neural crest in the bird has nothing to do with the development of nerves or ganglia, in consequence of which it is evident why the crest is largest in the region of the mid-brain. The massive production of mesodermic material appears where the widest part of the skull is to be formed.

GORONOWITSCH finds that, in association with true mesodermic cells, part of the neural-crest cells give rise to a »nervenführenden« tissue through which the true nerve fibres ultimately make their way. A proliferation of cells from the ectoderm into the mesoderm at the margin of the gill clefts is also noted.

This paper was followed by a short preliminary notice by JULIA PLATT ('93) of the formation of the branchial cartilages in *Necturus* from cells of ectodermic origin.

In the final paper of GORONOWITSCH ('93) we further find that the sheath of SCHWANN (page 212) arises from the nerve-supporting tissue which GORONOWITSCH describes as formed in part at least from cells of the neural crest, and it is suggested (page 216) that the mesenchyma-forming activity of the ectoderm in different regions of the head shows us that the origin of the cutis from the ectoderm is possible. Nothing is said regarding the origin of cartilage either in the branchial arches or elsewhere, but near the close of the paper (page 253) we read that the »periaxiale Stränge« may rather be associated with the development of the visceral arches than with the development of nerves, while on page 254, GORONOWITSCH adds, that he must leave for the present undecided whether the significance of the »periaxiale Stränge« in the development of the visceral arches consists merely in the fact that they form a part of the musculature of the arches. The »periaxiale Stränge« of GORONOWITSCH are composed of cells from two sources; dorsally of cells from the neural crest, and ventrally of cells proliferated from the mesoderm. The resultant tissue, however, is described as homogeneous.

The fate of the neural crest in the Teleostei, GORONOWITSCH finds similar to that of the neural crest in the bird.

The conclusions which I reach from the study of wandering ectodermic cells in *Necturus* differ widely from the conclusions reached by GORONOWITSCH in the study of the bony fish and bird.

Owing to a passing differentiation, occasioned by unequal absorption of yolk granules in the tissues of the head, the cells which

leave the neural crest and the external ectoderm in *Necturus*, do not form with wandering cells from the mesoderm, a homogeneous tissue, but remain for some time distinct.

An account of the origin of these cells, which I group together under the term mesectoderm, has been given in my first study on the ontogenetic differentiations of the ectoderm in *Necturus* ('94), and is reviewed at the beginning of the second division of the present paper under the heading Procartilage. In this first study, I followed the migrations of the cells of the mesectoderm until the stage of development in which these cells divide into two groups, one composed of nervous tissues, and the other of connective tissues. A second study ('96) was concerned with the development of the peripheral nervous system, while the present study discusses the further fate of that part of the mesectoderm which remains as connective tissue.

Part I and Part II of this study are separated by the appearance of true cartilage. In Part III those facts regarding the development of the branchial muscles, which have been noted in the first part of the study, in association with the development of the procartilage of the branchial arches, are brought together and extended, and the origin of the hypoglossal musculature is described, with a short discussion of the occipital segmentation. A few points of interest which appear in the second and third parts of the study, are noted in a summary at the end. The conclusions reached in the first part of the study — that concerned chiefly with the formation of procartilage — are discussed below, in the introduction, because of their direct bearing on the theoretical and actual value of the middle germ-layer.

I find that the branchial cartilages and the anterior part of the trabecular bars are formed in *Necturus* from mesectoderm, i. e. wandering cells of ectodermic origin. The posterior part of the trabecular bars, the basal plate of the chondrocranium, the auditory capsules, and the occipital arch are formed in mesenchyma of purely mesodermic origin. The mesectoderm appears to take no part in the formation of the endothelium of the blood vessels, nor does the mesectoderm take part in the formation of muscular tissue. It composes, however, the connective tissue which underlies the epithelium of the mouth at the time when the teeth first appear, and is consequently the source of the primitive dentine, not by direct proliferation from the epithelium of the mouth, as maintained by

KLAATSCH ('94) and denied by RÖSE ('94), but through the migration into this region of cells similar to those that form the basis of the branchial cartilages. Except for the cells that underlie the epithelium of the mouth, the mesectodermic part of the connective tissue is almost entirely consumed in the production of the branchial cartilages and the trabeculae. Those cells that remain become for me indistinguishable from wandering mesodermic cells, by which I would not imply that I believe them to form an identical tissue with the mesoderm. I know nothing further about them.

My conclusions concerning the fate of these wandering cells from the neural crest and external ectoderm in *Necturus* are compared below with the results obtained by GORONOWITSCH from the study of the neural crest cells in the bird.

According to GORONOWITSCH, the tissues which may be attributed to wandering ectodermic cells, chiefly from the neural crest, are:

- a) neither nerves nor ganglia, but
- b) mesenchymal tissue identical with that derived from the mesoderm,
- c) skeletogenous tissue from which the skull in the region of the mid-brain is formed,
- d) embryonic nerve-supporting tissue,
- e) the sheath of SCHWANN,
- f) possibly the cutis (from ext. ectoderm cells),
- g) possibly part of the musculature, at least, of the visceral arches.

The tissues derived from the mesectoderm in *Necturus* are:

- a) both nerves and ganglia,
- b) a connective tissue distinguished by yolk differentiation from the mesenchyma,
- c) skeletogenous tissue from which the branchial cartilages and anterior trabeculae are formed, but which takes no part in the formation of the skull in the region of the mid-brain,
- d) not embryonic nerve-supporting tissue, but embryonic nerves,
- e) ?
- f) dentine, but not the cutis,
- g) no musculature in the visceral arches or else-where.

An evident explanation of part, at least, of the differences in the above conclusions based on the study of the bird and of *Necturus*, is given by GORONOWITSCH when he says, that he absolutely loses the wandering ectodermic cells in the mesenchyma, and consequently

assumes that they form with the mesenchyma a homogeneous tissue. To my thinking inability to distinguish cells from the two sources by no means proves their identity, but should it be possible to distinguish the tissues in other Vertebrates, as in Amphibia or in Petromyzon, the inference is rather that a difference actually exists in forms where the cells appear, with our present methods of differentiation, absolutely alike.

Two interpretations of the phenomena connected with the development of the branchial cartilages in *Necturus* suggest themselves.

One may hold with KASTSCHENKO (loc. cit.) that the mesenchyma is a tissue composed of cells left over from the formation of epithelial tissues by any of the germ-layers, and that it is a matter of indifference which of the mesenchymal cells take part in the formation of any tissue, or whence the cells are derived. As favoring such a view one may regard the fact that the cartilage of the skull, including the posterior part of the trabeculae, although of mesodermic origin, apparently forms a homogeneous tissue with the cartilage of the branchial arches and of the anterior part of the trabeculae, which is of ectodermic origin. The fact that true bone arises from mesodermal cells, while the primitive dentine is derived in *Necturus* from the mesectoderm looks in the same direction.

On the other hand, were it a matter of indifference which cells of the mesenchyma form a given tissue, it is not easily explicable why the mesectoderm, which arises in the dorsal and dorso-lateral part of the head, should migrate en masse towards the ventral part of the head, while mesenchymal cells of mesodermic origin migrate in the opposite direction. As the two tissues pass one another, the mesectodermic cells lie to the outside, the mesodermic to the inside, and each tissue appears to maintain its independence. Those mesectodermic cells which compose the connective tissue thus appearing, not less than the cells which compose the peripheral nervous system, to have a definite purpose before them -- a purpose which requires a longer journey by a greater number of cells than is demanded by the peripheral nervous system of the embryo in this early stage of development.

A second view which may be held, is that the branchial cartilages and the anterior part of the trabeculae are not only ontogenetically, but also phylogenetically structures of ectodermic origin, possibly constituting with the notochord the primitive skeleton of the ancestral

Vertebrate, acquired before the mesoderm had assumed a share in the functions originally belonging to the ectoderm. It may be thought that the participation of mesectoderm in the formation of dentine tells against this view. However, the tooth, or placoid scale, stands on the border line where the external ectoderm first calls the lower tissue to its aid in forming a defensive skeleton, in which enamel, a product of the ectoderm, was first and originally the only hard substance (WIEDERSHEIM, '93, page 45).

This introduction does not claim the merit of an historical or critical review, since many works of importance, which might have been mentioned, have been omitted, while those of less accuracy have been coordinated with those of greater. My purpose has been to show the position which this study holds in relation to morphological questions still undecided, thus possibly justifying the detailed description which follows.

Part I.

Procartilage.

As the present study begins with a stage of development immediately following that with which my first study ('94) on the ontogenetic differentiations of the ectoderm in *Necturus* closed, I briefly review those facts recorded in the earlier publication which serve to explain the condition of the middle tissues in the head of the embryo about to be described.

a) In Review.

Prior to the closure of the neural folds in *Necturus*, one finds that the wings of axial mesoderm at the side of the chorda end anteriorly in the same transverse plane as the chorda itself. Anterior to this plane, the wall of the archenteron comes into immediate contact with the ectoderm, touching the floor of the neural plate medianly and forming laterally, by contact with the ectoderm at the side of the neural plate, the Anlagen of the hyomandibular clefts, which consequently do not break through the mesoderm, but are secondarily surrounded by mesoderm. A similar mode of formation of the anterior branchial clefts in *Petromyzon* is described by v. KUPFFER ('94).

Anterior to the extremity of the chorda, the dorsal wall of the archenteron gives rise to mesoderm primarily quite separate from

the wings of axial mesoderm at the side of the chorda¹. The dorsal wall of the archenteron is thus the source of that mesoderm which represents in *Necturus* the walls of the mandibular, praemandibular, and »anterior« head-cavities in the *Selachii*. These head-cavities, however, are not distinguishable in the endodermic mesoderm of *Necturus*.

In later development, the anterior mesoderm, thus proliferated from the dorsal wall of the archenteron, unites with the wings of axial mesoderm, both above and below the hyomandibular clefts, forming with the axial mesoderm an apparently homogeneous tissue.

In my first study on the differentiations of the ectoderm ('94, page 913), I assumed, on the authority of the majority, that the axial mesoderm, which arises at the margin of the blastopore, or in the line of the primitive streak, is morphologically a tissue of purely endodermic origin, and in distinction from later ectodermic additions to the »middle layer«, I called this presumably endodermic mesoderm »mesendoderm«. Subsequent study leads me to doubt whether the axial mesoderm can properly be regarded, even theoretically, as a derivative of the endoderm alone, and in consequence, I return to the familiar appellation »mesoderm«, using the term, however, to designate a tissue composed of cells of uncertain origin and affinities.

The neural crest in *Necturus* is interrupted between the trigeminal and facial Anlagen. Both parts of the crest fuse with thickenings of the ectoderm which occur in two longitudinal lines on each side of the head; in a dorso-lateral line which passes through the auditory epithelium, and in an epibranchial line, immediately above the dorsal margin of the gill clefts. Along both lines of ectodermic thickening cells are rapidly added to those of the neural crest constituting together a tissue, the mesectoderm, peculiarly distinguished in *Necturus* from the surrounding mesoderm by great reduction in the size of the yolk granules with which all of the embryonic tissues are primarily crowded. Similar ectodermic thickenings from which cells are added to those of the neural crest have been described by different authors in several classes of Vertebrates, and according to the detailed description of v. KUPFFER ('90, '91) the relations in *Petromyzon* closely resemble those in *Necturus*.

¹ This region of mesodermic proliferation is axial and does not extend laterally, relatively ventrally, to the region in which the mandibular arteries, seen in fig. 19, pl. XVIII, arise.

The mesectoderm forms in the trigeminal region, a wide sheet of tissue extending from the neuropore to the posterior boundary of the mid-brain, but the invagination of the auditory epithelium soon separates the facial mesectoderm from that in the region of the glossopharyngeus and vagus Anlagen. From their neural, dorso-lateral, and epibranchial lines of origin, the mesectoderm cells wander downwards immediately below the superficial ectoderm. On reaching the places where the ectoderm has fused with the endoderm to form the mouth or gill clefts, the mesectoderm, continuing its downward migration, turns inwards between the mesoderm and the endoderm, and thus finally comes entirely to surround the mesoderm of the branchial arches and to underlie the invaginated ectoderm on the anterior and posterior (ultimately dorsal and ventral) surfaces of the mouth.

Meanwhile the dorsal cells of the mesectoderm group themselves into the cranial ganglia, and become distinct from the connective tissue of which the ventral part of the mesectoderm is composed. This mesectodermic connective tissue receives further additions from the ectoderm in the neighborhood of the mouth and in the branchial arches.

Referring to my former paper (*loc. cit.*) for a more detailed account of the origin of the mesectoderm and its relation to the mesoderm in the head of *Necturus*, I now pass to the description of the stage of development with which this study begins.

b) Descriptive.

The Mesectoderm in *Necturus* 11 mm long.

My earlier study ('94) closed with the embryo 10 mm in length, and I begin this study with a stage of development immediately following, giving in fig. 1, pl. XVI, the head of an embryo 11 mm long. Figs. 1*a*—1*i*, show horizontal sections through planes indicated in fig. 1 by lines lettered to correspond with the letters below the respective sections figured. Throughout this series of sections, the several kinds of tissue are diagrammatically represented. The outlines of the tissues, however, were traced with the camera, and their relations are consequently accurate. The cells of the mesectoderm are represented in a solid shade, while the mesoderm cells are represented by circles. The cellular structure of the ectoderm and endoderm is not reproduced, as the series is given to show the

relation of the two middle tissues (mesectoderm and mesoderm) immediately before the differentiation which may be called the pro-cartilage stage.

Fig. 1*a* shows the most dorsal section of the series. At the left, the section passes through the floor of the auditory vesicle, and on the right slightly above the floor. The section cuts the anterior end of the notochord and the dorsal wall of the alimentary canal. The dorsal part of the third and fourth branchial clefts appears in section, but the plane of section lies above the dorsal margins of the first, second, and fifth clefts¹. The large ganglia of the glossopharyngeus and vagus nerves lie above the plane of section, and are now separate from the connective tissue component of the primitive mesectoderm, through the dorsal part of which the section passes, as this tissue begins to turn inwards at the dorsal margin of the branchial clefts.

The mesoderm seen in fig. 1*a* is chiefly composed of mesenchyma, but in each of the branchial arches a closer grouping of the cells gives rise to a mass of tissue (*mes*) more or less epithelial in character, which is the precursor of muscular differentiation. In each arch the mesectoderm nearly surrounds this mesothelial tissue.

The section of fig. 1*b* passes through the cavity of the branchial chamber. The anterior (dorsal) wall has fallen away from the mesoderm, as easily happens in preparations. The plane of section passes through the second and fifth branchial clefts in addition to those of the more dorsal section. The root of the trigeminal ganglion lies between the sections shown in figs. 1*a* and 1*b*, and the ganglion now (fig. 1*b*) appears in two divisions. The anterior part of the

¹ Although the hyomandibular cleft does not break through in *Necturus*, I begin my enumeration with this cleft, and also count the mandibular arch as the first branchial arch. The method of designating the whole series of arches »visceral«, and of beginning the enumeration of the »branchial« arches with the third visceral, meets with difficulties in comparative embryology since in Reptilia, Aves, and Mammalia, where embryonic arches also exist, the third visceral arch is not truly branchial, but, like the hyoid and mandibular arches, subserves merely secondary functions, while the third visceral arch is not the first branchial, i. e. gill-bearing, in the Selachii or Ganoidei (GENBAUR '78). I therefore prefer to follow BALFOUR ('85) in using »branchial« as coextensive with »visceral«, and shall designate the individual arches that lie posterior to the mandibular and hyoid, as the glossopharyngeal arch, the first vagus, and the second vagus, in correspondence with their primitive nerve supply, which is constant throughout the Vertebrata.

facial ganglion, seen at the left in the more dorsal section (fig. 1 *a*) has disappeared in fusing with the sensory epithelium of the supra-orbital line, and the posterior part of the ganglion lies in this section (fig. 1 *b*) near the mesothelial tissue of the hyoid arch. The mesothelial tissue of the hyoid arch, as well as that of the third, fourth, and fifth branchial arches, lies in the external and posterior part of the arch where it forms a cord of tissue extending vertically. The plane of fig 1 *b* sections transversely these cords of mesothelial tissue. Aside from the mesothelial cells, the posterior branchial arches also contain many scattered mesoderm cells that take part in the formation of the vascular system.

The mesectoderm in the region of the trigeminal and facial ganglia (fig. 1 *b*) lies chiefly near the external ectoderm, but several cells are also seen at the median side of the mesothelium of the hyoid arch. Above the plane of section, the external and median groups of mesectoderm cells are connected with one another, and in the embryo younger than that now described, the mesothelium of the arches is separated in its entire vertical extent from the external ectoderm by a layer of mesectoderm, and lies as a cord in the centre of a surrounding tube of mesectoderm. As development proceeds, however, the mesothelial tissue makes its way from the original, central, position towards the external and posterior surface of the arch, where it is seen in fig. 1 *b*.

In the posterior branchial arches, the same shifting of the mesothelium from its primary, central, position occurs, and the relations of the median branchial tissues to one another are further complicated by the migration of cells of the mesenchyma through the mesectoderm in consequence of the development of the vascular system, as the walls of the blood vessels are formed by cells of mesodermic (or endodermic) origin.

To show the great difference in the aspect of the two median tissues, mesoderm and mesectoderm, parts of three sections have been enlarged and colored as they appear when stained with BIONDI-EHRlich. The third branchial arch on the left of fig. 1 *b*, included in the line *b'*—*b'*, was chosen for enlargement in fig. 1 *b'*. On three sides of the figure, above, below, and at the right, are seen yolk-laden cells from the wall of the alimentary canal. The bounding tissue at the left is ectoderm. In the lower, left corner of the figure, an irregular group of yolk-laden mesoderm cells represents the mesothelial cord in transverse section, while scattered cells

with yolk granules at the right of this mesothelial tissue and in the walls of the vascular spaces form the mesenchyma of the section. Most of the cells of the mesectoderm lie between the vascular spaces and the wall of the anterior branchial cleft, a few cells, however, are seen at the left, just beneath the ectoderm, and near the mesothelium of the arch.

The section shows filaments of protoplasm, but few, if any, cell outlines are to be seen in the median tissues, and the number and position of the cells may be determined merely from their nuclei. The separation of the two median tissues is sharper in the mandibular or hyoid arches, where mesenchymal cells of the vascular system are not interpolated in the mesectoderm. Fig. 1*b'* does not show the most marked difference between the median tissues, but rather illustrates the manner in which the two tissues become entangled in the vascular region of the gill-bearing arches.

I have been accused of maintaining that the absence of yolk granules in the mesectoderm proves this tissue to be of ectodermic origin. Lest others than my accuser should also believe the accusation warranted, I take the present opportunity to say that I know the mesectoderm of *Necturus* to be of ectodermic origin because I have carefully followed the tissue from its origin, tracing the development through slight degrees of growth, in embryo after embryo, from the very beginning until the stage now described. The marked differentiation of tissues occasioned by difference in the size and quantity of the yolk granules, though proving nothing in itself, makes it possible to distinguish the median tissues of *Necturus* from one another with greater certainty than that with which they may be distinguished in any other Vertebrate embryo with which I am acquainted, although I am told that a similar differentiation occurs in other of the Amphibia.

The colored figures are not given to show that part of the median tissues is ectodermic, while another part is not. They are given that those who may not be able to examine *Necturus* embryos for themselves may see how apparent the difference between the two kinds of tissue really is.

Fig. 1*c* passes through the infundibulum and the dorsal part of the optic vesicles. The hyomandibular pocket approaches the ectoderm at the left of the section and touches the ectoderm on the right. The fifth branchial cleft has passed out of section, and of the fourth cleft only the ventral wall is seen. The compact group of mesoderm cells

posterior to the optic vesicle is from the dorsal part of the mesothelial tissue of the mandibular arch. The position of the neighboring mesectoderm cells is seen to be similar to that of the mesectoderm cells of the hyoid arch in fig. 1 *b*, or of the glossopharyngeal (third visceral) arch in fig. 1 *a*, since the respective sections cut these arches at nearly the same relative level. There are, however, a greater number of mesectoderm cells at the base of the mandibular arch than at the bases of the other arches, and unlike the mesothelium of the hyoid arch, the mesothelium of the mandibular arch is completely separated, at the level of the section, from the superficial ectoderm by intervening mesectoderm.

One notices chiefly in the hyoid arch the relatively large amount of mesothelial tissue, and the absence of large blood vessels. Otherwise the arrangement of the median tissues of the hyoid arch in fig. 1 *c*, is not unlike that in the third and fourth branchial arches of fig. 1 *b*.

In the third branchial arch of fig. 1 *c*, one finds the number of mesectoderm cells in the inner part of the arch greatly increased. This is partly, but not entirely, due to the obliquity of the plane of section in reference to the axis of the arch. There is, however, an actual accumulation of mesectoderm cells in the ventral part of the arch.

A similar increase in the number of mesectoderm cells is found in the fourth arch, moreover the mesectoderm of this arch is now, in fig. 1 *c*, united with that of the fifth arch near the wall of the pericardium. A small knob of cells on the antero-lateral wall of the pericardium is from the mesothelium of the fifth arch as it unites with the pericardium. The mesothelial tissue on the lateral wall of the pericardium, posterior to the knob of cells just mentioned, forms the anterior extremity of the ventral longitudinal muscles of the trunk.

Fig. 1 *g* passes through the middle of the eye and sections the floor of the branchial chamber. The small lumen in the wall of endoderm is a pocket from the alimentary canal which extends ventrally towards the mouth invagination. The entrance to the mouth is still entirely closed by endoderm, as seen from the following sections (figs. 1 *h* and 1 *i*). The anterior of the paired projections in the lateral boundary of the endoderm (fig. 1 *g*) indicate the position of the mouth, which lies ventral to them. The posterior projections are from the ventral walls of the hyomandibular clefts. On the left

of the figure, the endoderm of the cleft still touches the ectoderm. On the right the endoderm, in the plane of section, is separate from the ectoderm allowing the mesectoderm of the mandibular arch to join that of the hyoid. The position of the mesothelial tissue in the mandibular and hyoid arches is essentially the same as in fig. 1*c*, although, as the sections have become more ventral, the mesothelium of the mandibular arch has increased in quantity while that of the hyoid has slightly diminished.

Between sections 1*c* and 1*g*, the mesectoderm cells of the hyoid arch have increased in number, as did the mesectoderm cells of the third arch between sections 1*b* and 1*c*, moreover the mesectoderm of one side of the body has now united with that of the other, forming a bridge of mesectoderm below the floor of the branchial cavity. To explain more completely the relations in the posterior branchial region, figs. 1*d*, *e*, and *f* are inserted between figs. 1*c* and 1*g*. The sections follow one another dorso-ventrally in the alphabetical order of the letters by which the figures are designated.

In fig. 1*d*, the posterior part of the branchial cavity no longer falls in the plane of section and the walls of the third gill cleft are severed from their attachment to the floor of the branchial chamber. The median tissues of the third arch occupy relatively much the same position as in fig. 1*c*. In the fourth arch, the mesothelial tissue is united with the wall of the pericardium on the left, and is separated on the right merely by an intervening blood vessel.

In fig. 1*e*, the severance of the walls of the third branchial cleft from the floor of the branchial chamber, begun in the plane of fig. 1*d*, is complete, and the mesectoderm of the third arch now meets that of the fourth arch. The mesothelial tissue of the fourth arch has united on either side with the wall of the pericardium.

In fig. 1*f*, the mesectoderm of the third arch is not only united with that of the fourth arch, as in fig. 1*e*, but also with the corresponding mesectoderm of the opposite side of the head, forming a tissue that occupies the interval between the anterior wall of the pericardium and the receding floor of the branchial chamber, save where the space is held by blood vessels.

Returning to fig. 1*g*, one notices that the mesothelial tissue of the third arch, which was separate in fig. 1*f*, has now in turn fused with the wall of the pericardium, while the separation of the walls of the second gill-clefts from the floor of the branchial chamber allows the mesectoderm of the hyoid arch to unite with that of the

third arch. At either side of the head, the section (fig. 1 *g*) cuts a stem of the external gills, which has budded from the third branchial arch. Fig. 1 *c* passes through the base of a similar bud from the fourth arch.

The tissue included in the line *g'—g'*, is drawn with higher magnification in fig. 1 *g'*, and colored as it appears on the slide. The figure shows the ventral part of the right glossopharyngeal arch. Bounding the section above and at the right, one finds the endodermic wall of the second branchial cleft, which, at the level of the section, is separate from the floor of the branchial chamber. In the lower, right-hand corner of the figure, a mass of endodermic tissue, distinguished from the ectoderm by the number of yolk granules, forms part of the ventral wall of the third branchial cleft. The tissue with yolk granules in the centre and at the left of the figure is mesoderm. The mesectoderm is nearly or quite free from yolk.

Comparing fig. 1 *g'* with fig. 1 *b'*, one notices that the mesothelial tissue, which in fig. 1 *b'* occupies an excentric position at the outer and posterior part of the third branchial arch, retains its primitive axial position in fig. 1 *g'*, where the mesothelium of the arch, in uniting with the wall of the pericardium, changes from the vertical to the horizontal plane. Fig. 1 *g'* also shows that the mesothelial tissue of the third arch unites with the wall of a vascular space anterior to the pericardium as well as with the wall of the pericardium itself, forming together an apparently homogeneous mesoderm. This vascular space, the ventral aorta, or heart, is bounded, however, by cells at least in part of endodermic origin. The mesectoderm cells in fig. 1 *g'* are seen to be much more numerous than those of fig. 1 *b'*. The tissue they compose, moreover, is continuous in fig. 1 *g'*, while in fig. 1 *b'* it is somewhat broken by cells of the mesenchyma connected with the vascular system.

Fig. 1 *h* passes through the lower part of the optic vesicle, and shows the union of the mesothelial tissue of the hyoid arch with the wall of the pericardium. The endoderm of the section is a solid mass of tissue in which the mouth cleft has not yet appeared. On comparing this section with those immediately preceding, it is seen that the endoderm which adjoins the anterior pericardial wall in fig. 1 *e*, lies at some distance from the wall of the pericardium in figs. 1 *f* and 1 *g*, but now again in fig. 1 *h* comes into contact with the pericardial wall. Hence the bridge of mesectoderm which, in the region of the second and third branchial arches underlies the

floor of the branchial cavity, is bounded ventrally as well as dorsally by endoderm. These relations are more easily explained from the models soon to be described.

The mesothelial tissue of the mandibular arch, in fig. 1 *h*, has passed the outward bend in the lateral wall of the endoderm, opposite which it stood in fig. 1 *g*, and now lies posterior to the transverse plane of the mouth. In the mesothelium of the hyoid arch a small central cavity is seen. Although the mesothelial tissues of the several arches undoubtedly represent the walls of the branchial part of the body cavity, in *Necturus* the mesothelium of the branchial arches usually forms a compact cord of cells in which the central cavity is obliterated, save in the ventral part of the hyoid and mandibular arches.

In fig. 1 *h*, as compared with fig. 1 *g*, the number of mesectoderm cells has further increased, and their nuclei are more closely crowded together in the posterior part of the section, while in the anterior part of the section, scattered mesectoderm cells now replace the mesenchyma of more dorsal sections, save at the surface of the brain, which is bounded by a vascular network of mesenchymal cells i. e. scattered cells of mesodermic origin.

The section shown in fig. 1 *i* passes through the optic stalk at the right, and through the dorsal part of the nasal epithelium at the left. The endoderm extends to the lateral surface of the section, where the dorsal (ultimately posterior) margin of the mouth lies. The posterior prolongation of the endoderm seen in fig. 1 *h* has receded from the pericardial wall, and the short intervening space is occupied by cells of the vascular mesenchyma. The mesothelial tissue of the mandibular arch has fused with that of the hyoid, thus indirectly establishing its connection with the pericardial wall. A mandibular head-cavity is found on both sides of the embryo. The mesectoderm in the anterior part of the section, shown in fig. 1 *i*, includes more cellular elements than in fig. 1 *h*, but is constantly separated from the brain by an irregular line of mesenchyma. The scattered mesectoderm cells of the anterior part of the head gradually form a more compact tissue as they approach the anterior (dorsal) surface of the mouth, which now separates them from the mesectoderm of the mandibular arch.

The tissues included within the curved line *i'*—*i'* of fig. 1 *i*, are colored and enlarged in fig. 1 *i'*. At the left this figure is bounded by ectoderm, in which the yolk granules are not yet entirely absor-

bed, although sufficiently reduced to distinguish the ectoderm sharply from both endoderm and mesoderm. Near the upper margin of the figure, a row of deep ectoderm cells are pushing their way inwards to form the posterior (ventral) lining of the buccal cavity. Between these ectoderm cells and those likewise pushing inwards to form the anterior (dorsal) epithelium of the mouth, a thin layer of endoderm extends to the surface of the head. To the layer of endoderm thus enclosed, the yolk granules which bound the upper surface of the figure bear witness. The line where the ectodermic cells of the epithelium lining the mouth meet the endodermic cells of the branchial cavity is sharply marked by yolk differentiation. The yolk-laden tissue at the bottom of the figure is from the wall of the pericardium, and is continuous with the mesothelium of the mandibular arch, which occupies the centre of the figure. Between the wall of the pericardium and the endoderm of the mouth one or two mesenchymal cells are found.

It will be noticed that a few yolk granules are scattered through the mesectoderm, the tissue which nearly surrounds the mesothelium of the mandibular arch. It is possible that these granules belong to cells which have not yet absorbed their primitive supply of yolk, but it is more probable that the granules have been washed onto the mesectoderm from a neighboring tissue, since large yolk granules are apt to float off when the slide is passed through aqueous solutions, and may then become again attached to the slide as it is withdrawn from the vessel in which the solution is contained. However this may be, the difference between ectoderm and endoderm is not more sharply marked than that between mesoderm and mesectoderm. It should be recalled that the yolk differentiation becomes evident when the mesectodermic cells are still at that stage of development in which they are recognized, described, and figured, by every embryologist who presents a study of the development of the Vertebrate nervous system, as composing a tissue of ectodermic origin, the Anlage of the cranial ganglia. From that earlier stage until the present, the sharp yolk distinction between the two kinds of median tissues is always found. After the present stage, however, the yolk differentiation of the median tissues rapidly disappears through the reduction of the yolk granules contained in the mesoderm.

The first series of figures ends with fig. 1 *z*. The branchial region has nearly passed out of section, and with it the region in which the trabeculae first appear. After a few sections, the right

and left ridges of ectoderm, seen in fig. 1 *i*, just anterior to the pericardial wall, meet and sever the mandibular arches from the wall of the pericardium. The point at which the mesothelial tissue of one side of the head becomes continuous with that of the other side is carried farther forward as the plane of section becomes more ventral, until the mandibular mesothelium passes out of section, and the outer mesectoderm of the mandibular arch becomes continuous in the median plane. As seen from fig. 1, the antero-ventral part of the head continues in section for some time, but as this part of the head, which ultimately becomes the antero-dorsal, is not directly concerned with the formation of cartilage, it seemed unnecessary to continue the series of figures beyond the plane of fig. 1 *i*.

Hoping to make the relations of the median tissues of the head clearer, I also give in figs. 2 and 3, drawings from models which were made from cross-sections through an embryo 10 mm long. Fig. 2 represents the mesectoderm, and fig. 3, the branchial endoderm. I chose for reconstruction an embryo slightly younger than that from which sections 1 *a* — 1 *i* were made, in order to show more primitive relations in the hyoid and mandibular arches.

Although fig. 2 shows the space relations of the mesectoderm, it fails to give an idea of the density of the tissue represented. Thus the anterior mesectoderm of the head forms a reticulum with relatively large interspaces, while the mesectoderm that bounds the epithelium of the mouth, and that which occupies the ventral part of the branchial arches, is a dense tissue composed of continuous protoplasm, one might almost say composed of nuclei, so close to one another do the nuclei lie. The mesectoderm of the dorsal branchial region is intermediate in density, but mesectoderm of one density passes gradually into that of another. To supply these density relations which the model fails to give, one may refer to the sections.

Fig. 2 does not represent the entire mesectoderm, but merely the connective tissue which remains after the nervous part of the primitive mesectoderm has been deducted. The model consists of eleven incompletely separated parts, belonging respectively to the anterior head region, and to each half of the five branchial arches. It is viewed in fig. 2 from the ventral surface. If one imagines the model thus seen revolved on its long axis until the lateral surface faces the observer, and then imagines the long axis inclined so that

the left end is higher than the right, it may possibly be fitted in imagination to the embryo of fig. 1, so that the relation of the mesectoderm to the surface of the embryo becomes more evident.

The fore-brain passes over the curved anterior margin of the mesectoderm (fig. 2 *f.b*). The depressions marked »*n*« are where the thickened nasal epithelium indents the underlying tissue. Above the nasal indentations, the margin of the mesectoderm is hollowed out as the tissue passes around the eye. Along the margin marked »*oph*«, the main branch of the ophthalmicus profundus trigemini lies. This ganglionic nerve is formed like the proper cranial ganglia from cells cut off from the dorsal part of the mesectoderm. From the anterior extremity of the figure to the hyomandibular cleft, the tissue may be called »trigeminal«, since derived from that anterior part of the neural crest, which, with its secondary ectodermic additions in dorso-lateral and epibranchial lines, gives rise to the ganglionic cells of the trigeminal group in its dorsal part, and to the mesectoderm of the anterior part of the head and of the mandibular arch in its ventral part.

Throughout the space marked »*m*« (fig. 2) the ectoderm and endoderm have fused. In the anterior, wider, part of the space, the mouth ultimately appears. The posterior, narrower, part of the space gradually closes by the continued growth in an anterior direction of the tissues that unite the right and left halves of the mandibular arch ventrally. The oral fusion of ectoderm and endoderm is primarily throughout an axially elongated space from which there are no transverse, or lateral, extensions, such as are found at the anterior part of the fusion in fig. 2. As the oral fusion extends laterally it becomes reduced posteriorly so that the mouth finally breaks through in the transverse plane. In the embryo of fig. 2, the fusion of the mesectoderm of each half of the mandibular arch with that of the opposite side has just begun.

The anterior part of the trigeminal mesectoderm, which is partly separated from the posterior or mandibular part by the oral fusion, has united widely (fig. 2) with the corresponding mesectoderm of the opposite side of the head, forming a shell of tissue, that is separated from the floor of the anterior part of the brain merely by a thin layer of reticular mesenchyma, and which lines the ectoderm of the anterior (dorsal) wall of the mouth. Figs. 1 *c*, *g*, *h*, and *i*, show that the trigeminal mesectoderm gradually approaches the axial plane on the anterior wall of the buccal cavity. In sections immediately

following fig. 1 *i*, the mesectoderm of one side of the head unites with that of the other.

At the dorsal margin of the branchial arches the mesectoderm of each arch is separate from that of the neighboring arches, in the stage of development which the model represents. This separation is transitory, and more or less unimportant since the fusions taking place between the cranial ganglia are in fact unions of the dorsal elements of the mesectoderm, while the later union of the branchial cartilages above the gill clefts is not less a fusion of mesectodermic elements. Moreover, at the stage given in fig. 1, the mesectoderm above the hyoid arch is continuous with that above the mandibular arch. Below the hyomandibular cleft the mesectoderm of the mandibular arch fuses with that of the hyoid, both in the outer and inner part of the arch (see fig. 1 *h*), while the mesectoderm in the posterior and median part of each half of the hyoid arch unites with the corresponding mesectoderm of the opposite side forming the bridge of tissue seen in fig. 1 *g*. The hyobranchial cleft completely separates the mesectoderm of the hyoid and third arches, although the mesectoderm forms a continuous tissue at the ventral margins of the posterior clefts. In the slightly older embryo from which sections 1 *a*—1 *i* were made, the hyoid mesectoderm is united with that of the third arch below the hyobranchial cleft. Primarily the mesectoderm of each arch is separate until in its downward migration the ventral margin of the gill cleft has been passed.

The central cavity or core of each arch is filled by mesothelium which joins the pericardial wall where the mesectoderm of the several arches ends. The anterior wall of the pericardium lies between the transverse bridges of mesectoderm connecting the right and left halves of the hyoid and mandibular arches. I have mentioned that the core of mesothelial tissue ultimately leaves its central position, and breaks through the surrounding mesectoderm at the posterolateral part of the branchial arches, where, on the posterior arches, the external gills are borne. This change in the position of the mesothelium had not occurred in the embryo modeled.

Above the vagus arches lie the anterior myotomes of the body, while the mesoderm above the remaining arches consists chiefly of mesenchyma surrounding the notochord, brain, and cranial ganglia.

Fig. 3 shows the outer surface of the endoderm of the head from a lateral and somewhat ventral aspect. The unshaded strips at the mouth and branchial clefts indicate the fusions between ecto-

derm and endoderm. The T-shaped oral fusion at »m« lies in the space »m« of fig. 2, and is bounded posteriorly by the transverse mandibular bridge of mesectoderm. The successive branchial pockets extend at their lateral margins both higher and lower than the dorsal and ventral walls of the branchial chamber from which they arise. The hyomandibular cleft is exceptional in ending ventrally in the lateral wall of a median ventral outgrowth from the floor of the branchial cavity.

This outgrowth, the thyroid Anlage, sectioned in fig. 1 *h*, lies between the transverse mesectodermic bridges of fig. 2. The hyoid bridge is dorsal to the outgrowth, and the mandibular ventral, but between the thyroid outgrowth and the mid-ventral part of the mandibular mesectoderm lies the mesothelial tissue of the united hyoid and mandibular arches, as seen in fig. 4, which represents a cross section through the thyroid outgrowth in an embryo slightly younger than that modeled in fig. 2. As fig. 4 is drawn with a higher magnification than that used in figs. 1 *a*—1 *i*, the tissues are less diagrammatically represented. The nuclei of both mesoderm and mesectoderm are outlined, while the yolk granules are represented by dots. The section is bounded above by the anterior wall of the hyobranchial cleft. Immediately below this endodermic wall lie mesectoderm cells of the hyoid arch. Those of one half of the arch have just come in contact with those of the opposite half, and as yet the uniting bridge is but one cell deep. The centre of the figure is occupied by the thyroid outgrowth, below which the section passes through a wide pocket of mesothelial tissue from the median part of which, the mesothelium of the mandibular arch extends forwards, while the lateral part of the mesothelial pocket is continued dorso-laterally into the hyoid arch. Cells from the posterior margin of the mandibular bridge of mesectoderm are seen below this mesothelial tissue. The central cavity in the thyroid outgrowth is continuous with the cavity of the branchial chamber. At its posterior extremity the outgrowth meets the anterior wall of the pericardium, and in this region ultimately gives rise to the thyroid gland. The anterior part of the outgrowth becomes irregularly broken, and part of the cells are finally lost in the mylohyoid muscle¹.

¹ PAUL BUJOR ('91, page 82) claims that in *Petromyzon* part of the muscles of the lingual piston and pharynx come from cells derived at metamorphosis from the disintegrated thyroid and velum.

The Mesectoderm in *Necturus* 12 $\frac{1}{2}$ mm long.

The figures numbered 5 *a*—5 *e*, pl. XVII, are from a series of horizontal sections through an embryo 12 $\frac{1}{2}$ mm in length. They represent sections through the branchial arches and show that the mesectoderm cells begin to group themselves more densely in definite regions. In the embryo of 11 mm (figs. 1 *a*—1 *i*), the mesectoderm cells in the ventral part of the branchial arches are much more numerous than in the dorsal part, but show little or no tendency to accumulate in limited spaces within the arches they occupy. In the embryo of 12 $\frac{1}{2}$ mm, this tendency, however, becomes evident.

Although the series of sections shown in figs. 5 *a*—5 *e*, are given for comparison with the sections of fig. 1, it is not possible to give planes that exactly correspond, since the head, bent downwards in the younger embryo, as seen from fig. 1, begins to rise into the plane of the long axis of the trunk. The readjustment is not achieved by bending in any one transverse plane, but affects the relative position of all of the structures of the head.

In the series 5 *a*—5 *e*, pl. XVII, I give no sections corresponding to the planes of figs. 1 *a* and 1 *b*, although in the older embryo, mesectoderm cells have begun to group themselves near the inner, endodermic, wall of the branchial arches in the plane corresponding to that of fig. 1 *b*. It is probable that the downward migration of mesectoderm has been continuous, since this tissue has greatly increased in the ventral part of the branchial arches. The mesothelial tissue of the gill arches is still distinguished by yolk granules, although less conspicuously than in the younger embryo, and it is further found that the cells of this tissue now begin to elongate into muscle fibres. The change from an embryo of 11 mm to one of 12 $\frac{1}{2}$ mm is not so great as to allow extensive displacement or replacement of tissues, and it is therefore perfectly possible to see where the tissues sharply distinguished in the embryo of 11 mm still lie.

I have found it impracticable to continue the diagrammatic manner of distinguishing the median tissues adopted in the series 1 *a*—1 *i*, partly because the cells in the older embryo have become much smaller through repeated division, so that their representation on the scale adopted for clearness of distinction in figs. 1 *a*—1 *i*, is even less in accordance with the actual size of the cells as compared with the other space relations of the section. The method is also

impracticable because the separation between mesectoderm and mesenchyma (i. e. wandering cells of mesodermic origin) is uncertain in the older embryo, while the differentiation of the mesothelium into muscular tissue gives a new means of distinguishing this tissue from the mesectoderm.

Comparing figs. 5 *a* and 1 *c*, one notices that the planes of section correspond only approximately. Both sections pass through the infundibulum and through the dorsal part of the eye, but while fig. 1 *c* shows the mesothelium of the mandibular arch, the plane of fig. 5 *a* passes above the dorsal limit of this tissue. The region occupied in fig. 1 *c* by the mandibular mesothelium and the surrounding mesectoderm, is occupied in fig. 5 *a* by tissue distinguished from the remaining reticular tissue of the anterior part of the section by the closer grouping of the component cells, and also by the entire absence of yolk granules which still distinguishes the mesectoderm from the adjacent mesenchyma, although the line of demarcation is no longer as sharp as in the younger embryo.

In the hyoid arch the mesothelial tissue, seen in fig. 1 *c*, has given rise to the large hyoid muscle, anterior to which in fig. 5 *a*, lies the hyoid nerve. The migration of the mesothelial tissue towards the posterior wall of the arch, begun in the younger embryo, has continued, and in consequence the mesectoderm of the older embryo occupies only the anterior part of the arch. The walls of the posterior branchial arches have expanded laterally with the growth of the external gills, and the arc described by the mesothelial tissue of the arches has increased in length correspondingly. Although all of the muscular tissue in the branchial arches arises from the primitive mesothelium, all of the mesothelial tissue does not give rise to muscle cells, and one finds that part of the space once occupied by the mesothelial cord is ultimately occupied by vascular tissue. In the glossopharyngeal arch, the mesectoderm cells in the inner part of the arch have increased in number in the older embryo (fig. 5 *a*), while the more open tissue which occupies the external part of the arch appears to be formed by cells of mixed origin.

In the first vagus arch, fig. 5 *a* shows the cord of mesothelial tissue as it bends inwards towards the pericardium. In sections through more dorsal planes, this muscle band is sectioned transversely and occupies the same relative position as the muscle band of the glossopharyngeal arch in fig. 5 *a*. The mesothelial tissue of the vagus arch, like that of the glossopharyngeal arch, has also an

increased arc of extension in the older embryo. Median to the fourth branchial cleft, fig. 5 *a* shows the suprapericardial bodies. The fifth branchial cleft lies dorsal to the plane of section as in fig. 1 *c*.

At the left fig. 5 *a* shows the union of the base of the muscle band of the second vagus arch with the muscular tissue on the wall of the pericardium, corresponding to the knob of mesothelial tissue on the antero-lateral wall of the pericardium in fig. 1 *c*. The plane of fig. 5 *a* passes posteriorly through a median depression in the floor of the alimentary canal. The mesectoderm uniting ventrally the first and second vagus arches on each side of the body in fig. 1 *c*, is united in the median line with that of the opposite side in fig. 5 *a*, showing that the axial fusion of the mesectoderm, begun with the hyoid bridge in the embryo of 10 mm (fig. 2) and extending to the glossopharyngeal arch in the embryo of 11 mm, now extends to the first vagus arch.

Fig. 5 *b* shows a section through the middle of the eye, and may be compared with fig. 1 *g*. In place of the mandibular mesothelium posterior to the eye in the younger embryo, we find now the large mandibular muscle from which a prolongation extends inwards to the wall of the branchial cavity. The nature of the cells grouped closely just posterior to the muscle, and through which the attenuated mandibular artery passes may be determined by comparison with fig. 1 *g*, where the only cells in the region in question are distinctly mesectodermic. The floor of the hyomandibular cleft is seen in fig. 5 *b*, while external to this prolongation from the wall of the branchial cavity, the mesectoderm of the mandibular arch unites with that of the hyoid arch, as on the right in fig. 1 *g*. The hyoid mesothelium has developed into the hyoid muscle, which begins to separate into two distinct parts, an inner thicker part, the muscle cerato-hyoideus externus, and an outer thinner part, the muscle mylo-hyoideus. Median to the hyoid muscle, and in the angle formed by the bases of the hyomandibular and hyobranchial pockets, the mesectoderm cells are closely grouped. The planes of figs. 1 *g* and 5 *b*, in both the younger and older embryos, pass through the mesothelium, or muscular tissue, of the glossopharyngeal arch as it unites with the wall of the pericardium. In the older embryo, however, an outgrowth from the mesothelium of the glossopharyngeal arch extends forwards towards the wall of the hyobranchial cleft. This is the beginning of the muscle cerato-hyoideus

internus, which is thus seen to be a muscle belonging to the third branchial arch. The mesectoderm of the glossopharyngeal arch now begins to show a closer grouping of the cells in the anterior part of the arch.

In fig. 5 *b*, the median bridge of mesectoderm extends from the branchial floor to the wall of the pericardium, and the cells begin to be more closely grouped in the axial line, between the two vascular spaces. The third branchial cleft lies above the plane of section, but its position is indicated by elevations in the ectoderm posterior to the hyobranchial cleft. As the embryo grows the branchial clefts bend backwards from the transverse plane in which they open outwards in the younger embryo, and this deflection is most marked in the hyobranchial cleft. From comparison with fig. 1 *g*, it seems probable that some of the cells bounding the anterior wall of the branchial cavity (the mouth) in fig. 5 *b*, are of ectodermic origin. The difference between the mesectodermic and mesodermic tissues in the older embryo, however, is not sufficiently marked to enable me to determine with certainty which of the cells in this region belong to the mesectoderm.

Fig. 5 *c* gives the transition from fig. 5 *b* to fig. 5 *d*, showing that below the plane of fig. 5 *b*, when the hyobranchial clefts have passed out of section, the dense mesectoderm of the hyoid arch becomes continuous from side to side. Fig. 5 *c* further shows that below the plane in which the mesothelium of the glossopharyngeal arch unites with the pericardium, the mesectoderm cells of this arch and those in the axial line between the median vascular spaces, are widely separate where in fig. 5 *b* they were closely grouped. The mandibular muscle in passing beyond the transverse plane of the oral pocket loses its connection with the wall of the branchial chamber and becomes entirely surrounded by mesectoderm, which is most dense in the angle between the oral pocket and the floor of the hyomandibular clefts.

Fig. 5 *d*, like fig. 1 *h*, shows a section through the lower part of the eye, and through the point where the mesothelial or muscular tissue of the hyoid arch unites with the wall of the pericardial cavity. Median to the point of union, in the older embryo, two muscle bands extend forwards to the floor of the branchial chamber. These muscles form the anterior extremity of the ventral longitudinal muscle of the trunk, and their origin is described in the third part of this paper. The section given in fig. 5 *d*, shows the present

length of the muscles, which increases as the embryo grows, until, as muscles *genio-hyoidei*, they extend to the anterior extremity of the lower jaw.

The mesectoderm, which in fig. 1 *h* is evenly dense in the space between the mesothelium of the mandibular and hyoid arches, is seen in fig. 5 *d*, to be more dense in the neighborhood of the mandibular muscle, while the cells about the hyoid muscle have become more scattered. The mouth is still entirely closed by endoderm. The mesectoderm cells on the anterior and posterior surfaces of the invaginated oral ectoderm are more closely grouped than in the younger embryo. In the plane of fig. 5 *d*, there is no doubt that the cells bounding the antero-lateral margin of the oral epithelium are mesectodermic.

The plane of fig. 5 *e* passes through the dorsal wall of the nasal epithelium. If the section be compared with fig. 1 *i*, it is seen that the mesectoderm cells, which in fig. 1 *i* are closely grouped in the angle where the superficial ectoderm turns inwards to form the anterior (dorsal) epithelium of the mouth, compose in the older embryo, a comparatively dense tissue in the same relative position. Posterior to the mouth the relation of the tissues is somewhat changed. The united mesothelial tissues of the hyoid and mandibular arches, seen in fig. 1 *i*, have been converted into the muscle *mylo-hyoideus* in the older embryo, and the mesectoderm cells which surround the mesothelium in fig. 1 *i*, are now grouped more densely in the antero-lateral region of the mandibular arch, while the median cells of this arch, and those of the hyoid arch, have become more scattered. A slight constriction in the lateral surface of the section indicates the plane of separation between the hyoid and mandibular arches. Fig. 1 *i'* shows that in the younger embryo, the mesectoderm in the anterior part of the mandibular arch had already begun to become more dense than in the posterior or hyoid part of the section.

I trust that comparison of the two series of sections, figs. 1 *a*—1 *i* and 5 *a*—5 *e*, suffices to show that the mesothelial tissue of the branchial arches has given rise to muscle cells, and that where the surrounding cells are most closely grouped in the older embryo they may be traced by their relative position to mesectoderm cells of the younger embryo, which are separated sharply from cells of the mesoderm by the absence of yolk granules. The origin of these cells which are free from yolk, I have described in a former study

('94), and know to be ectodermic, yet I doubt if it be possible to convey to others by means of a few sections selected from two or three series, the conviction one feels who has studied entire series from nearly two hundred embryos in successive stages of development. As the mesectoderm is not shut off from the mesenchyma by a limiting membrane, the cells composing the two tissues come into immediate contact, and the possibility that some cells from the mesenchyma lose their yolk and join those arising from the ectoderm cannot be excluded, any more than such a possibility can be excluded in the case of the cranial or spinal ganglia, which also are not at first sharply separated from the surrounding mesenchyma. One can only say that there is no positive evidence that such cells do add themselves to the mesectoderm, as might be furnished, for example, by an intermediate condition in the appearance of the cells along the line where one tissue meets the other. Moreover, the comparison of the relative number of cells in the two tissues, and of their grouping, in closely successive stages demonstrates absolutely that if there has been any addition to the mesectoderm of cells from the mesenchyma, they have been very few in number.

It should be remembered that in the earliest stage in which wandering cells comparatively free from yolk are found, these cells lie in the dorsal and dorso-lateral part of the head, and that later such cells are not found in this region, save the relatively small number taking part in the formation of the nervous system, but are found in the ventral part of the head, while intermediate stages show the cells in intermediate positions.

The Procartilage in *Necturus* 15 mm long.

I now pass to the description of the branchial arches in an embryo of 15 mm. No true cartilage has yet appeared, but the primitive position and shape of each cartilaginous bar is definitely determined by compact masses of cells, whose nuclei surrounded by very little protoplasm compose a peculiar tissue called »procartilage«. The superficial cells of the prochondral bars thus formed, are in places flattened against the body of the bar, showing that a perichondrial differentiation begins to be established. This happens especially where but few mesectoderm cells intervene between the surface of the bar and the neighboring mesodermic or endodermic tissues. In such regions, the beginning of a perichondrial layer seems to show that the growth of the prochondral bar by accretion

of neighboring cells has here ceased. More frequently, however, the prochondral tissue passes gradually from the compact structure of the bar into the less compact surrounding tissue, indicating that in these regions growth by aggregation of more scattered mesectoderm cells continues.

Figs. 6 *a*—6 *e*, pl. XVII, from horizontal sections through the branchial region of an embryo 15 mm in length, are given for comparison with figs. 5 *a*—5 *e*. The plane of section inclines upwards from right to left, but because of the slight obliquity seemed to offer better opportunity for comparison, since the changes in the relative position of the tissues due to lifting the head into the plane of the long axis of the embryo have been considerable, and sections through an embryo of 12½ mm do not exactly correspond with those through the embryo of 15 mm.

Fig. 6 *a* shows a section which passes through the optic stalk on the right, and below the median plane of the eye on the left. The group of prochondral cells posterior to the optic stalk, and the corresponding opposite group, are from the anterior horns of a primitive plate of tissue which underlies the brain. With these horns the anterior parts of the trabecular bars fuse, but the cells that compose the horns are not mesectodermic. A small group of cells, *trh*, at either side of the hypophysis in fig. 5 *a* are from these anterior horns of the basi-cranial plate at an earlier stage of development, when the cells that are to form the anterior part of the trabeculae are still indistinguishable in the mesectoderm which bounds the mouth anteriorly.

Since the plane of fig. 5 *a* passes above the mandibular muscle, the relation of this muscle to the prochondral cells of the mandibular bar in fig. 6 *a* and 6 *b* may be compared with the relation of the muscle to the closely grouped mesectoderm cells of the mandibular region in fig. 5 *b*, or the position of the mandibular muscle and the procartilage at the left in fig. 6 *a* might better be compared with the corresponding tissues in fig. 1 *c*. In regard to the mesectoderm cells that lie external to the mandibular mesothelium in fig. 1 *c*, I am unable to say whether they become absorbed in the procartilage which arises posterior to the mandibular muscle, or continue their migration downwards.

The hyoid muscle and procartilage in fig. 6 *a* may be compared with the corresponding tissues in fig. 5 *a*. The muscular tissue still occupies the posterior part of the arch, but on the right in fig. 6 *a*

is divided into the muscle *cerato-hyoideus* within and the *mylo-hyoideus* without. The region in which the hyoid procartilage lies is occupied in the younger embryo (fig. 5 *a*) by mesectoderm.

At the left in fig. 6 *a* are seen the prochondral bars of the glossopharyngeal arch and of the first and second vagus arches, the two latter being united at their bases. On the right the figure shows the common base in which all three bars unite. If the glossopharyngeal and first vagus arches in fig. 6 *a* be compared with those of fig. 5 *a*, it is seen that the muscle band still lies against the posterior wall of the arches, while the procartilage bars at the left in fig. 6 *a* are readily traced to the dense mesectoderm of fig. 5 *a*, although the third branchial cleft in the plane of fig. 5 *a* is still connected with the floor of the branchial chamber, from which the cleft has just parted in the plane of fig. 6 *a*, as indicated by the enlargement at the median extremity of its ventral wall. The plane in which the glossopharyngeal mesectoderm unites with that of the vagus arches, corresponding to the union of the procartilage in these arches, falls between figs. 5 *a* and 5 *b*, and consequently lies dorsal to the union of the glossopharyngeal muscle with the wall of the pericardium which is shown in fig. 5 *b*. The union of the mesectoderm of these arches is seen, however, in fig. 1 *e*.

The plane of fig. 6 *b* passes through the eye at the left, and through the dorsal wall of the nasal invagination at the right. The procartilage of the trabeculae is seen near the optic stalks. The procartilage and muscular tissue of the mandibular arch occupy the position of the corresponding tissues in fig. 5 *b*. The hyoid muscle (fig. 6 *b*) is represented by the *cerato-hyoideus* and *mylo-hyoideus*. A median bar of procartilage connects the right hyoid bar with the united bars of the glossopharyngeal arch, although the left arm of the hyoid bar is still separate in the plane of section. This median prochondral bar is derived from the median mesectoderm, seen in fig. 5 *b* to extend from the wall of the branchial chamber to the wall of the pericardium between the median vascular spaces. Anterior to the muscle of the glossopharyngeal arch, the plane of fig. 5 *b* sections the ventral part of the mesectoderm that composes the procartilage of the glossopharyngeal arch seen in fig. 6 *b*. The union of the mesectoderm of this arch with that of the axial bar lies above the plane sectioned in fig. 5 *b*.

With the lengthening of the hyobranchial cleft by growth of the surrounding tissues, the muscle *cerato-hyoideus internus* has

increased in length. In fig. 6 *b*, the anterior extremity of the right *m. cerato-hyoideus internus* is seen on the inner wall of the hyobranchial cleft. It will be remembered that this muscle arises from the base of the mesothelial tissue of the glossopharyngeal arch. The lateral part of the muscle of the glossopharyngeal arch lies against the posterior wall of the arch.

On the inner wall of the third branchial cleft there is a small muscle that arises from the basal part of the mesothelial tissue of the first vagus arch. This muscle is called by MIVART ('69), who follows FISCHER ('64), the first constrictor arcuum.

A second small muscle seen on the right in fig. 6 *b*, just posterior to the first constrictor arcuum, represents the second and third constrictor muscles (MIVART, loc. cit.), which are as yet united. This muscle appears to arise from cells that separate from the anterior part of muscular tissue developed from the external (somatic) wall of the pericardium, but the muscle may also include cells from the basal mesothelium of the second vagus arch. The innervation of the muscle indicates that such is the case, and that one of the two parts into which the muscle ultimately divides, namely the smaller part, or third constrictor arcuum of MIVART and FISCHER (loc. cit.), is serially homologous with the first constrictor arcuum, and with the muscle *cerato-hyoideus internus*, while the larger part of the muscle, the second constrictor arcuum of MIVART and FISCHER, is a derivative of the somatic wall of the pericardium, receiving its innervation from three branches of the vagus nerve.

In fig. 6 *c*, the procartilage of the mandibular arch is seen, and in the plane of section the prochondral bar of the hyoid arch is continuous. The muscular tissue of the mandibular arch occupies nearly the same position as in fig. 5 *c*, while the dense mesectoderm of this arch in the younger embryo is replaced by procartilage in the older. The mesectoderm that bounds posteriorly the floor of the branchial cavity and the wall of the hyomandibular cleft in fig. 5 *c* gives rise to the procartilage of the hyoid arch seen in fig. 6 *c*. Between the sections shown in figs. 6 *b* and 6 *c*, the procartilage of the glossopharyngeal arch has passed out of section, and merely the anterior extremity of the bar that connects the procartilage of this arch with that of the hyoid is seen. The muscles of the hyoid arch in fig. 6 *c* resemble those of fig. 6 *b*. In the glossopharyngeal arch the *cerato-hyoideus internus* is sectioned at the left (fig. 6 *c*)

and near the wall of the pericardium the section also passes through the left constrictores arcuum.

Median to the nasal epithelia, fig. 6 *d* shows the procartilage of the trabeculae, here formed from the mesectoderm on the anterior wall of the mouth. A relatively small part, however, of the dense mesectoderm which bounds the mouth anteriorly takes part in the formation of the trabecular bars. The thyroid outgrowth from the floor of the branchial chamber, which is seen in fig. 5 *d*, lies just dorsal to the plane of section figured in 6 *d*, where a fragment of the outgrowth, however, is seen at the left of the muscle genio-hyoideus. The region of the mandibular and hyoid arches seen at the left in fig. 6 *d*, corresponds closely to that seen in fig. 5 *d*. The dense mesectoderm at either side of the mandibular muscle in the younger embryo has given rise to the corresponding procartilage of the older embryo. In the hyoid arch, the muscle mylo-hyoideus of fig. 6 *d*, occupies the same relative position as in fig. 5 *d*. The surrounding mesectoderm cells have become less numerous in the older embryo owing to the aggregation of these cells in the procartilage of the hyoid arch. At the right, in fig. 6 *d*, the mandibular muscle passes into the mylo-hyoideus. Although more mesectoderm cells immediately take part in the formation of the procartilage of the mandibular arch than in the formation of the trabeculae, the cartilaginous bars of this arch by no means exhaust the mesectoderm that bounds the mouth posteriorly.

In fig. 6 *e*, the relation of the cells in the trabecular region resembles that in fig. 6 *d*. The mandibular mesectoderm, seen posterior to the mouth in fig. 5 *e*, has given rise in the older embryo to the mandibular bars of procartilage seen in fig. 6 *e*. The position of the mylo-hyoid muscle is similar in both sections.

The three series presented in figs. 1 *a*—1 *i*, 5 *a*—5 *e*, and 6 *a*—6 *e* cover those stages of development in which the sharply differentiated mesectoderm of the branchial arches in the embryo of 11 mm is converted into procartilage in the embryo of 15 mm.

Aside from the procartilage of the branchial arches, a plate of peculiar tissue underlies the brain of an embryo of 15 mm, which resembles the procartilage of the branchial arches in also giving rise to true cartilage. The entire plate, however, is not converted into cartilage, although it seems primarily composed of a homogeneous tissue. This tissue differs in appearance from the procartilage of the branchial arches in that the cells of which it is composed

still contain large yolk granules, while their nuclei are separated from one another much farther than are those in the procartilage of the branchial arches. In both tissues there is, however, a protoplasmic differentiation, which is peculiar to procartilage. It readily stains, but does not resemble the clear matrix of true cartilage.

The basicranial plate, above described, extends from the first spinal nerve, the anterior of the two hypoglossus nerves, to the infundibulum, becoming gradually broader, but varying in depth. It lies a short distance below the floor of the brain, and is prolonged, on either side of the infundibulum, in an anterior horn which extends forwards and downwards. The chorda runs through the long axis of the plate, but does not reach its anterior limit by several sections. The depth of the plate, except near the anterior extremity, is less than the diameter of the chorda whose sides it bounds. The chorda thus divides the plate into two halves united with one another anteriorly. The two anterior horns of the plate form the posterior part of the trabecular bars. The procartilage of the anterior part of the trabeculae is mesectodermic, resembling that of the branchial arches, yet the transition from the anterior mesectodermic procartilage of the trabecular bar to the mesodermic procartilage of the anterior horns of the basicranial plate is not sharply marked. As indicated by the distribution of yolk granules the point of union between the two kinds of tissue lies just posterior to the optic stalk.

Fig. 10, pl. XVIII, is drawn from a sagittal section through the head of an embryo of 14 mm, in which the yolk granules have not yet disappeared from the mesoderm. The section passes to one side of the long axis of the embryo, and through the region where the anterior horn of the basicranial plate unites with the mesectodermic part of the trabecular bar. The nuclei are represented in the figure by circles and the yolk granules by dots. Anterior to the posterior part of this bar of procartilage (*tr*), the lateral wall of the infundibulum is seen. Anterior to the ventral, or anterior, part of the bar lies the optic stalk. In the axial plane, the convex wall of the infundibulum meets the basicranial plate, which lies above the hypophysis, as seen in fig. 7 *b*, pl. XVIII, a transverse section through the anterior extremity of the basicranial plate in an embryo of 15 mm.

Although the basicranial plate and its anterior horns are mesodermic in origin, while the cells that compose the anterior part of the trabeculae are of ectodermic origin, when true cartilage appears and the yolk granules are no longer found, I am unable to distinguish

the two kinds of tissue that make up the continuous and apparently homogeneous cartilaginous bar, which extends from the auditory capsule to the end of the snout.

In describing the development of the branchial arches in Triton, STÖHR ('80, page 482) tells us that here also an almost entire absence of yolk granules is a characteristic indication of the Anlagen of the visceral skeleton. STÖHR does not trace the origin of these cells so free from yolk, but notices that the other tissues of the head equally free from yolk are the brain and the cranial ganglia. In Siredon, according to STÖHR (loc. cit. page 490) quantities of yolk and pigment granules are found in the Anlagen of the visceral skeleton and trabeculae, but in Siredon pigment granules are also found in large quantities in the brain and ganglia, although absent in the Anlagen of the muscles. This further mark of similarity between the brain, the cranial ganglia, and the procartilage of the visceral arches, seems to me of interest in view of the fact that the tissues so similar have been traced in Necturus to a common origin, the ectoderm.

STÖHR also calls attention to the difference found in Triton between the anterior and posterior part of the trabeculae respecting the quantity of yolk granules, and to the fact that cartilage first appears in the anterior part of the trabecular Anlagen, and is then lost in the neighborhood of the eye-muscles, where yolk granules are found, but appears again further back in the tissue that lies at the side of the chorda. There seems consequently to be an interruption in Triton in the formation of the trabecular cartilage which corresponds to the point where, in Necturus, the ectodermic and mesodermic tissues of these bars unite.

Fig. 7, pl. XVIII, shows a model of the procartilage in the head of an embryo of 15 mm. The model was reconstructed from cross-sections, of which five are represented in figs. 7 *a*—7 *e* chiefly to show the position of the trabeculae and basiscranial plate, and to bring the branchial cartilages into relation to the structures which lie above them. The horizontal sections given in figs. 6 *a*—6 *e*, from an embryo of the same length, serve to show the relation of the branchial cartilages to one another, to the branchial clefts, and to the ventral musculature.

In Fig. 7, the branchial procartilages are seen from their ventral surface. Beneath them lies the basiscranial plate ending in the trabecular bars, which extend downwards and forwards. The trabecular

bars are not united with one another ventrally, but are connected dorsally with the basiscranial plate. The mandibular bars are separate from one another ventrally and are also separate from the basiscranial plate; they extend, however, dorsalwards to the horizontal plane of this plate. In fig. 8, pl. XVIII, the procartilage of the mandibular arch is seen in side view. The quadrate, which appears almost separate from the procartilage of MECKEL's bar, is, however, united with the bar by means of closely grouped mesectoderm cells that fill the space between the dotted line, seen in fig. 8, and the surface of the bar. Although these cells are not as yet differentiated into procartilage, they ultimately form cartilage.

The remaining branchial procartilages may be said to lie in one transverse plane, so slightly do the bars curve upwards. This plane is removed from that of the basiscranial plate by a distance equal to the length of the median bar between the procartilage of the hyoid and glossopharyngeal arches. The hyoid procartilage consists of a single curved bar united in the centre to a median longitudinal bar that forms a cartilage which FISCHER ('64) calls the »body of the hyoid«, and which HUXLEY ('74) distinguishes as the »first basibranchial« in *Menobranchus* (*Necturus*). This designation is also applied by STÖHR and WIEDERSHEIM to the corresponding cartilage in other Urodela.

The procartilage of the glossopharyngeal arch is also a single curved bar. Posterior to the centre of the bar there is a knob of tissue that develops into the Zungenbeinstiel of FISCHER (loc. cit.) or the second basibranchial of HUXLEY and WIEDERSHEIM (loc. cit.). The development of the glossopharyngeal cartilage does not support FISCHER's view that the bar in *Menobranchus* (*Necturus*) contains elements from two arches, since the cells that compose it belong from the first to the third branchial arch alone.

The bars of the vagus arches do not meet in the median plane, but the bars of the first vagus arch extend backwards from the lateral part of the glossopharyngeal bar, while the bars of the second vagus arch extend backwards from those of the first arch.

The differentiation in the mesoderm at the side of the chorda which forms the basiscranial plate is not sharply limited either laterally or posteriorly. It gradually becomes apparent anterior to the first spinal nerve. This nerve, which possesses a ganglion, but has merely a ventral root, lies median to the third myotome (4th postotic segment). The procartilage of the occipital arch (fig. 7) rises from

the basicranial plate in the intersegment between the second and third primitive myotomes, or third and fourth postotic somites. The first somite posterior to the ear, relatively below the ear, in the primary divisions of the mesoderm segmentally related to the glossopharyngeal nerve and to the third visceral arch, does not develop a proper myotome, but soon becomes scattered in mesenchyma.

In the transverse planes of the myosepta posterior to the occipital arch, the mesenchyma at the side of the chorda dorsalis and spinal cord begins to form a more compact tissue in preparation for the neural arches soon to appear. In the embryo of 15 mm, there is as yet no cartilage.

Fig. 9, pl. XVIII, shows the ventral aspect of a model of the wall of the branchial chamber in an embryo of 15 mm. From comparison of this figure with fig. 3, one sees the changes in the shape and position of the branchial clefts that are correlated with the conversion of mesectoderm into procartilage. The first transverse fold, seen at the right in fig. 9, represents the oral fusion. Anterior to this fold lie the trabeculae and almost immediately posterior lie the mandibular bars. The second transverse fold, representing the hyomandibular cleft, does not now extend to the surface of the embryo as in the earlier stage of development shown in fig. 3. The median outgrowth from the floor of the branchial chamber, the thyroid Anlage, still extends backwards from the floor of the united hyomandibular pockets to the wall of the pericardium. Dorsal to the anterior extremity of the thyroid outgrowth, and beneath the hyomandibular fold, lies the centre of the hyoid bar, from which the »horns« extend on each side outwards and backwards to the angle where the hyomandibular fold is lost in the wall of the branchial chamber. The »first basibranchial« lies in the axial plane immediately beneath (dorsal to) the thyroid outgrowth, and extends backwards between the floor of the branchial chamber and the third endodermic fold, seen in fig. 9, under the median part of which the first basibranchial unites with the bar of the glossopharyngeal arch.

The third transverse fold is formed by the hyobranchial clefts, which are not at first united, but extend directly outwards, as seen in fig. 3. Later, the tissues of the hyoid arch grow backwards forming a kind of operculum, and the direction of the hyobranchial clefts changes accordingly from the transverse plane to an oblique one. As the hyobranchial clefts change their direction, the external part of the clefts elongates ventrally, until the two clefts meet and

fuse with one another, so that the external opening is one wide cleft extending from side to side of the head. The opening of the branchial chamber to the exterior by means of the hyobranchial clefts is still retained in the embryo of 15 mm, although the thin walls that bound the clefts are closely applied to one another, and form in section hardly more than a line through the surrounding tissues. Fig. 7 *d* shows a transverse section through the region in which the hyobranchial clefts are united in one wide cleft.

The »horns« of the bar of the glossopharyngeal arch come from beneath the hyobranchial pockets, between these pockets and those of the third branchial clefts. The ventral margins of the third clefts now meet the external opening of the united hyobranchial clefts. Between the third and fourth clefts lie the bars of the first vagus arch, which pass forwards ventral to the point where the third clefts meet the hyobranchial, and here fuse with the bar of the glossopharyngeal arch. The fourth cleft lies between the two vagus bars. The fifth cleft, which is not included in the figure, lies between the second vagus bar and the trunk of the embryo. This cleft is small, and still lies in a plane nearly transverse to the long axis of the embryo.

In fig. 7 *a*, which represents a section through the mesectodermic part of the trabeculae, I would call attention to a closer grouping of the cells in the neighborhood of the trabeculae, between the eye and the dorsal wall of the mouth. These cells are mesectodermic, and ultimately give rise to the antorbital process.

Fig. 7 *b* shows a section through the anterior extremity of the basiscranial plate. Although at this stage of development the tissue which composes the plate seems homogeneous, true cartilage forms only in the posterior part of the plate and in the lateral margins of the anterior part. That part of the plate which surrounds the point of the chorda disappears without giving rise to skeletal tissues. The procartilage of the quadrate and of MECKEL'S bar is seen in fig. 7 *b*, and between these two elements of the mandibular arch lies the mandibular muscle. The ventral part of the section passes through the anterior part of the mylohyoid muscle. A diverticulum from the floor of the branchial chamber is formed by the united bases of the hyomandibular pockets (compare fig. 9), and the median space thus surrounded by endoderm is the anterior part of the hyoid arch.

In fig. 7 *c* a section is seen, which passes through the anterior part of the auditory vesicle. Here the basiscranial plate is divided

by the chorda into two halves. The width and depth of the plate is less than in fig. 7 *b*, and its outline is less regular. Below the floor of the branchial chamber, the section passes through the first basibranchial in the axial plane, and through the hyoid bar at either side. The lateral part of the hyomandibular pocket lies external to this bar of procartilage (see fig. 9), while internal to the bar are seen the dorsal extremities of the hyobranchial clefts. On the lateral wall of the hyomandibular cleft lies the posterior part of the mandibular muscle. Below the basibranchial bar, the thyroid outgrowth is seen in transverse section, while the wide mylohyoid muscle underlies all.

A group of cells seen in fig. 7 *c* below the auditory vesicles, gives rise to the first cartilage of the auditory capsule. I have not included the tissue which these cells compose in the model of the procartilage, although it somewhat resembles that of the basicranial plate. Figs. 11 and 12, pl. XVIII, are from transverse sections through the auditory vesicle and the surrounding tissues, before the constrictions that ultimately divide the vesicle have appeared, and before the yolk granules have disappeared from the mesoderm. The section seen in fig. 11 is from an embryo about 10 mm in length. The auditory vesicle is here bounded on the left by the facial (auditory) ganglion, and below by closely grouped mesoderm cells that lie at the head of the mesothelial tissue of the hyoid arch.

Fig. 12 is from an embryo of 13 mm, and shows the opposite vesicle to that seen in fig. 11. As the magnification in figs. 11 and 12 is the same, it is evident that the auditory vesicle is much larger in the older embryo. The epithelium in the vicinity of the facial (auditory) ganglion has become deeper, while the ventral wall of the vesicle has become thinner. In the younger embryo (fig. 11) the closely grouped mesoderm cells below the ear form an apparently homogeneous tissue with the mesothelium of the hyoid arch, in which no muscle fibres have yet developed. In the older embryo (fig. 12), the tissue in question is differentiated into two parts. In the ventral part muscle fibres have appeared continuous with those of the hyoid arch, while the dorsal part of the tissue is separated off as a plate of procartilage underlying the ear. To this plate as a centre of growth, mesoderm cells soon add themselves, enveloping the lateral wall of the auditory vesicle with a single layer of cartilage-forming cells. In the embryo from which a section is shown in fig. 12, these lateral cells have not yet differentiated from the surrounding mesenchyma.

Fig. 7 *d* shows also, in lower magnification, the plate of procartilage underlying the auditory vesicle and dorsal to the hyoid muscle. In this figure the basiscranial plate is narrower but deeper than in the preceding figure of the series (7 *c*), and now closely invests the lateral surface of the chorda. The section passes through the region in which the hyobranchial clefts are united (see fig. 9). In the centre of the tissue enclosed between the united hyobranchial clefts and the floor of the branchial chamber, the thyroid outgrowth is sectioned, dorso-lateral to which are seen the large procartilage bars of the glossopharyngeal arch. Attached to the ventral surface of these bars, the cerato-hyoideus internus is seen in section, while below the thyroid outgrowth the paired muscles genio-hyoidei are sectioned. Beneath the hyobranchial cleft lies the wide mylohyoid muscle.

The plane of fig. 7 *e* passes through the procartilage of the occipital arch. At the base of this arch, the chorda is bounded by procartilage from the posterior part of the basiscranial plate. The large vagus ganglia are sectioned and the second postotic myotome, that of the third postotic segment.

With the description of figs. 7 *a*—7 *e*, from the series of sections from which the procartilage represented in fig. 7 was modeled, the first part of this study closes.

The purpose of the foregoing pages has been to show, by detailed comparison of section with section, that from the mesectoderm, a tissue surrounding the mesothelium of the branchial arches, and bounding the epithelium of the mouth, in the embryo of 11 mm, the cartilage of the visceral skeleton and of the anterior part of the trabeculae arises, while the remainder of the cartilaginous skull finds its origin in the mesoderm.

It has also been my purpose to show that the mesothelium of the branchial arches is converted into muscular tissue. In the third part of this paper, I shall show to which part of the mesothelium each muscle of the head may be traced, and shall there bring together those scattered facts regarding the myology of the head which have appeared in the preceding study of successive sections.

Before passing to the consideration of the cartilaginous stage in the development of the skull, I call attention to the fact that the origin of the anterior part of the trabeculae from the same kind of tissue (mesectoderm) as that which gives rise to the visceral

skeleton lends support to the view that the trabeculae were primarily bars of a prae-oral visceral arch.

SEWERTZOFF ('97, page 422) notes that in embryos of *Acipenser*, *Petromyzon*, and of the *Amphibia*, where the mesocephalic flexure of the brain is slight, the trabeculae lie in a position nearly horizontal, while in those animals which have a pronounced mesocephalic flexure, as in the *Selachian* embryo, the trabeculae are almost vertical. From this correlation between cranial flexure and direction of the trabeculae, SEWERTZOFF concludes that the primary function of the trabeculae was that of supporting the brain.

I regret that SEWERTZOFF does not tell us the position of the mouth cleft in these embryos, for should it appear that the trabeculae are horizontal in position when the mouth cleft, dorsal (relatively anterior) to which they lie, is horizontal, and vertical when this cleft is vertical, a correlation might be found leading to quite different conclusions.

SEWERTZOFF, moreover, includes the *Amphibia* among those forms in which, with slight mesocephalic flexure of the brain, the trabeculae lie almost horizontal. I believe no power of imagination could lead one to describe the procartilage, camera outlined in fig. 8, as a nearly horizontal bar. When this bar of procartilage is converted into cartilage, it does, indeed, lie horizontally, but so also do the mandibular bars which bound the mouth cleft ventrally (relatively posteriorly), yet their horizontal position proves nothing against the primitive branchial function of the bars.

Part II.

The Cartilaginous Skull.

The anatomy of the skull in *Menobranchus* (*Necturus*) has been described by HUXLEY ('74), and the development of the Urodel skull, as observed in *Triton* and *Siredon*, has been carefully studied by STÖHR ('80). In the following account, I shall consequently note chiefly such points as seem to me of some importance, wherein the development of the skull in *Necturus* differs from that of *Triton* and *Siredon*, as described by STÖHR, attempting to make this part of the study merely supplementary to the admirable papers of HUXLEY and STÖHR, rather than complete in itself.

The order of development.

True cartilage is first found in the embryo 17 mm long, and appears in the course of the trabeculae, extending from beneath the optic stalks through the antero-lateral margins of the basicranial plate. STÖHR ('80, '82) tells us that in Triton, Siredon, and in the Anura, the cartilage of the visceral skeleton appears before that of the trabeculae, or remaining skull. The chondrification of the trabecular bars in *Necturus* is immediately followed by that of the prochondral bars in the visceral arches. The bars of the mandibular, hyoid, and glossopharyngeal arches chondrify almost simultaneously. Those of the vagus arches somewhat later. In the meantime cartilage appears in the occipital region of the skull, with which the cartilage of the trabeculae in its backward growth unites forming the basal plate. The auditory vesicles then become gradually surrounded by cartilage, which becomes connected with the basal plate through the chondrification of intermediate tissue, primarily in the form of two pairs of connecting bridges, which, becoming wider in antero-posterior extent, meet and fuse with one another, while the anterior extent of the basal plate is further increased by a third cartilaginous connection with the auditory capsule anterior to the facial ganglion. Cartilaginous partitions appear in the internal chamber of the auditory capsules with the development of the semicircular canals. The trabeculae extend forwards and become connected with one another anteriorly by an internasal plate, while from each trabecular bar an antorbital process grows laterally. The posterior part of the brain becomes roofed by a band of cartilage connected with the dorsal part of the united auditory capsule and occipital arch. In no case is the development of one of these cartilaginous elements of the skull complete, however, before the development of other cartilaginous elements begins. Finally a cartilaginous support for the nasal membrane and a cartilaginous ring about the eye arise independently, while a number of fusions occur between cartilaginous elements originally separate.

The basal plate¹.

The cartilage first found on each side of the head in the course of the trabeculae, is separate from every other skeletal element,

¹ I distinguish the prochondral plate lying below the brain, from the cartilaginous plate found here in later stages of development, by calling the

but in its backward growth soon meets the side of the chorda near the transverse plane passing through the middle of the auditory vesicles. Anterior to this plane, the median prochondral tissue of the basicranial plate disappears, and the chorda extends free nearly to the posterior wall of the hypophysis. In Triton, according to STÖHR ('80), the trabecular plates meet at each side the point of the chorda, which they soon surround anteriorly, occupying thus that area of the basicranial plate which in *Necturus* does not chondrify. In the Anura (STÖHR '82), although the trabecular plates ultimately surround the point of the chorda, at first the chorda extends forwards completely free beyond the region in which its sides are enclosed by the trabecular plates, as is permanently the case in *Necturus*. This condition in *Necturus*, however, is evidently secondary, as evinced by the disappearance of the antero-median part of the basicranial plate.

Fig. 14, pl. XVIII, is a diagram showing the early relations of these tissues. The procartilage of the basicranial plate is bounded posteriorly by the line *b—b* and terminates anteriorly in two horns that reach as far forwards as the optic stalks, or to the line *a—a*, where they pass into the mesectodermic part of the trabeculae, indicated in the diagram by dotted outlines. Although the trabecular bars are here represented as lying in the plane of the basicranial plate, in reality they curve downwards as seen from the sagittal section shown in fig. 10, pl. XVIII, or from the model shown in fig. 7.

The position of the membranous ear is indicated in the diagram, and two short cross-lined bars extending on the right from the basicranial plate towards the auditory vesicle show the position of the first two fusions taking place between the cartilage of the ear, and the basal plate. In the embryo of 17 mm, the tissue about the ear is still unchondrified. The connection between the auditory capsule and basal plate occurs in the embryo of 18 mm, when the anterior, posterior, lateral, and ventral walls of the capsule (save the foramina) are chondrified, but while the median and dorsal walls of the capsule are still open. The anterior of the two connecting bars forms first. It lies immediately posterior to the egress of the ramus hyomandibularis facialis from the facial ganglion,

former »basicranial«, the latter »basal«. The two plates are not coextensive, and consequently do not represent the same plate in successive stages of cartilaginous development.

and connects the auditory capsule with the trabecular part of the basal plate. The posterior bar arises from the region which STÖHR ('80) calls the »mesotic« part of the basal plate, and fuses with the auditory capsule at its inner, posterior margin. The relations of this bar of cartilage will be further discussed in connection with the description of the chondrocranium in *Necturus* 46 mm long. Fig. 28, pl. XVIII, shows a transverse section through the anterior bar. Gradually the space between the two connecting bars closes, and the floor of the auditory capsule becomes throughout continuous with that of the basal plate. Meanwhile a second connection between the trabeculae and the auditory capsule appears anterior to the facial ganglion, so that the rami hyomandibularis and palatinus then pass outwards through foramina in the floor of the skull.

When chondrification takes place in the basicranial plate, the prochondral tissue is gradually transformed into cartilage, the clear matrix of which is first found in the mesodermic part of the trabecular bars, and extends thence both forwards and backwards, leaving, however, the triangular area which surrounds the point of the chorda unchondrified (fig. 14). While this anterior region of chondrification is extending backwards through the procartilage of the basicranial plate, a second paired area of chondrification appears in the occipital region, where the clear matrix of cartilage is also soon found. These posterior centres of chondrification lie at the base of the occipital arch in the same horizontal plane as the chorda, although not in immediate contact with the chorda.

The paired Anlagen of the anterior and posterior regions of the head, are at no time sharply limited towards one another, but each passes gradually into the intervening procartilage of the basicranial plate which soon chondrifies in its median part in continuity with both anterior and posterior areas of chondrification. There is consequently an intermediate area in the plate where chondrification takes place slightly later than near the two extremities, but two pairs of distinct cartilages, the homologues respectively of the »Balckenplatten« and »Occipitalplatten«, described by STÖHR ('88) in *Triton*, are not found in *Necturus*.

Although the procartilage of the basicranial plate is deeper in those transverse sections which pass near the point of the chorda and in those through the occipital region, than in the intermediate space, as seen by comparing figs. 7 *b*, 7 *d*, and 7 *e* with fig. 7 *c*,

the plate is evidently unsegmented. This fact should not be regarded as supporting the view of GEGENBAUR ('72), GOETTE ('75) and WIEDERSHEIM ('77) regarding the elemental unity of the basal plate of the skull. The procartilage of the branchial arches is also unsegmented, although each cartilaginous arch, except the posterior, is composed of distinct segments. The relation of procartilage to cartilaginous segmentation, is similar to that of the axial mesoderm to metameric segmentation. Both tissues supply the unsegmented material on which the future segmentation is stamped.

In the Anura, STÖHR ('82) tells us, there exist in the basal plate of the skull at an early stage of development, three pairs of thicker cartilaginous elements, which are at no time completely separate, being from the first connected with one another by thinner tracts of cartilage. The anterior pair of cartilaginous elements are the trabecular plates, the median pair, STÖHR calls the »mesotic« cartilages, while the posterior pair are the occipital plates, the »parachordalia« of HUXLEY, or enlarged bases of the occipital arch. In the cartilage which in Triton connects the auditory capsules with the axial part of the basal plate, STÖHR finds the homologue of the mesotic elements of the Anura.

In the development of the basal plate, Necturus occupies, in some respects, an intermediate position between the Urodela described by STÖHR (Triton and Siredon) and the Anura. As in Triton, cartilage first appears in the trabeculae, then in the occipital region, extending from these Anlagen through the intervening space. Unlike Triton, however, in Necturus, these cartilaginous elements are not at first distinctly separate, but as in the Anura, the primitive Anlagen pass into one another, so that there is actually but one pair of plates, separated by the chorda.

The cartilage of the auditory capsules arises independently in Necturus, and parachordal cartilage is not associated with the periotic in the formation of the floor of the capsule. PARKER ('76) also finds the otic capsule in the Urodela independent of the basal plate, and GOETTE ('75) claims that this in the case in Bombinator, but GAUPP ('93) tells us that in Rana, the floor of the auditory capsule is in part formed from parachordal cartilage.

The first procartilage of the auditory capsule, as shown in Part I, arises in tissue continuous with the mesothelium of the hyoid arch, seen at an early stage in fig. 11, pl. XVIII. In the later development represented in fig. 12, this mesothelial tissue is separated into

two parts. In the ventral part muscle fibres begin to form, while in the dorsal part procartilage arises. This plate of procartilage lies primarily ventral to the floor of the ear, but is carried laterally with the development of the ear, and as cartilage forms, comes to lie below the floor of the external semicircular canal. This later position of the plate is shown in fig. 28, where the ground shade also indicates that from the plate as a centre of chondrification, cartilage is gradually extending dorsalwards.

In *Necturus* the tissue occupying the space between the floor of the capsule and the basal plate becomes gradually converted into cartilage in such manner that one cannot speak of this cartilage as properly an outgrowth either from the parachordal or periotic cartilage. The uniting cartilage includes in its formation indifferent cells of the mesenchyma lying between the basal plate and the auditory capsules, which give rise to cartilage without passing through the procartilage stage. A similar direct conversion of cells of the mesenchyma into cartilage in this region in *Triton* has been noted by STÖHR ('80).

The skull in *Necturus* 19 mm long.

Figs. 15 and 16, pl. XVIII, represent a model of the cartilaginous skull in an embryo of 19 mm, in which the cartilaginous elements of the head are well established. In fig. 15, the skull is viewed from the ventral surface, showing chiefly the branchial bars, which, with the exception of those of the mandibular arch, have been omitted in fig. 16, where one views the chondrocranium from the side and from above. Merely a closer grouping of cells indicates the position of the internasal plate which later connects the trabecular bars anteriorly; and the antorbital processes, although outlined in the figures, are as yet unchondrified, still consisting of the closely grouped nuclei that characterize procartilage — here mesectodermic.

The trabecular bars are round or oval in section, thus resembling the primitive form of these bars in the *Anura* more closely than in *Triton* or *Siredon*, where according to STÖHR ('80) the trabeculae are from the first nearly vertical plates at the side of the brain. From fig. 17 it is seen that the trabecular bar, a short distance posterior to the antorbital process, is connected in three places with a short dorsal bar of cartilage lying parallel to the trabecula, thus leaving two spaces surrounded by cartilage. Through the anterior of these openings the optic nerve passes outwards. Through the

posterior opening, there pass a blood-vessel and the nerve oculomotorius.

The cartilage of the dorsal bar, with that of the vertical bars which connect this bar with the trabecula, forming together the crista trabeculae, arises in prochondral tissue that appears to be composed of cells which have migrated dorsalwards from the prochondral Anlage of the trabecular bar. The cartilage of the dorsal bar, however, is not at first connected with the trabecular cartilage, but fuses posteriorly with the ascending process of the quadrate cartilage before becoming connected with the trabecula by means of the cross bars that bound the openings for the optic and oculomotor nerves. In the embryo modeled, the middle bar, although represented in fig. 16, was still prochondral.

STÖHR ('80) says that in Triton the orbital wall of the skull arises in connection with the trabeculae, and not independently as GOETTE ('75) is inclined to think of general occurrence. SEWERTZOFF tells me that he considers the independent origin of this dorsal bar of cartilage significant as indicating a possible homology with the large alisphenoid cartilage, recently described by SEWERTZOFF ('97) in the Selachii, or with a similar structure described by SALENSKY ('78) in Acipenser.

The quadrate, although primarily connected by procartilage with the cartilage of MECKEL'S bar, chondrifies independently, and at the stage of development represented in fig. 17 (19 mm), has fused with the dorsal bar of the crista trabeculae alone. The mandibular bars, which are paired, even in the procartilage stage (fig. 7), are now connected with one another anteriorly merely by procartilage, indicated in fig. 15 by the dark band uniting the anterior extremities of the bars.

If fig. 15 be compared with the figure of the adult branchial cartilages in Menobranchus (Necturus) given by HUXLEY ('74), it is found that each branchial element already exists as a distinct cartilage. Although the mesectoderm of which the prochondral bars are formed is of paired origin, the prochondral bars themselves are not paired in the hyoid and glossopharyngeal arches, as seen from fig. 7. However, when the procartilage is converted into cartilage, each cartilaginous element of the arches arises as an independent area of chondrification, separated by procartilage from the neighboring cartilaginous elements.

The body of the axial bar called the »first basibranchial«,

chondrifies before the posterior extremity of the bar, so that the cartilage of this bar is at first separated from the cartilage of the cerato-branchial bars of the third visceral arch by the unchondrified procartilage of the posterior extremity of the basibranchial bar. When cartilage arises in the posterior part of the first basibranchial, this cartilage is divided into right and left halves separated in the axial plane by procartilage. Each half, however, is directly continuous anteriorly with the undivided cartilage of the body of the bar, and posteriorly each half adjoins the corresponding cerato-branchial of the third arch. This relation seemed of interest as tending to justify the name given to the first axial bar, by showing it to be, at least in its posterior part, composed of basal elements from the third visceral arch. There is an early stage of development when the cartilage of each cerato-branchial of the third arch is directly continuous with the cartilage of the corresponding half of the posterior extremity of the first basibranchial. From the fusion of adjacent cartilages, however, little may be inferred regarding their primitive relations to one another.

The second basibranchial is not formed in the same kind of tissue, mesectoderm, as the remaining branchial bars, but arises from cells on the anterior wall of the pericardium which are mesodermic, although it is probable that a few cells at the proximal end of the bar come from the mesectoderm. The bar arises later than the remaining branchial cartilages, and I am inclined to doubt the serial homology implied in its name, »second basibranchial«, and to regard the bar as a foreign element associated secondarily with the branchial arches.

The dorsal, relatively lateral, margins of the cartilaginous bars of the three posterior arches, are connected with one another above the gill clefts by procartilage, indicated in fig. 15 by dark bands.

No fusion has yet taken place between the quadrate cartilage and the auditory capsule. GAUPP says ('93, page 434) »some false statements of GOETTE, such as the participation of the ascending process in the formation of the lateral wall of the skull have already been set right by STÖHR«, and STÖHR does indeed say ('80, page 492), that in the Urodela studied by him no such participation in the formation of the wall of the skull can be ascribed to the quadrate. In *Necturus*, nevertheless, the ascending process actually does bound the brain laterally, thus forming part of the skull-wall, as maintained by GOETTE ('75).

In the embryo 19 mm long, the inner wall of the auditory

capsule is developed only in its dorsal part and at the anterior and posterior margins. Through the posterior and smaller of the two notches, seen in fig. 16 in the margin of the inner wall of the capsule, the ductus endolymphaticus passes dorsalwards from out the otic chamber. The trigeminal ganglion lies between the auditory capsule and the quadrate cartilage. The roots of the facial and auditory ganglia are median to the large opening in the inner wall of the auditory capsule, through which the auditory nerves pass directly to the membranous ear, while the hyomandibular and palatine branches of the facial nerve accompany the auditory nerve into the capsule, passing outwards through the two anterior of the three openings in the floor of the capsule, seen in fig. 15, the smallest opening being that for the palatine nerve. The ganglion of the facial element of the lateral-line system lies median to the anterior part of the inner wall of the auditory capsule, the nerves from the ganglion passing dorsalwards and forwards near the trigeminal ganglion. Median to the posterior wall of the capsule lie the roots of the glossopharyngeal and vagus nerves, which pass outwards through the space between the occipital arch and the auditory capsule.

The posterior and largest opening in the cartilaginous floor of the auditory chamber is that of the fenestra ovalis. The position of this opening is seen in transverse section in fig. 17, where it is also seen that were the inner wall complete, the auditory capsule would form in section a nearly equilateral triangle with rounded corners. As testified by all who have employed modern methods of study, the fenestra ovalis is not a secondary opening in the cartilaginous case of the ear, but is from the first merely closed by a membrane.

At the stage represented in fig. 15 (i. e. 19 mm in length), the operculum¹ is unchondrified, and is not shown in the model. The Anlage, however, is already established in procartilage, and one finds that the operculum in *Necturus*, is neither part of the primitive otic capsule, nor formed in the membrane closing the fenestra. It arises independently. STÖHR ('80) tells us that in *Triton* and *Siredon*, the operculum is an outgrowth cut off from the margin

¹ I regret the employment of the term »operculum« to designate structures so widely different as the covering of the gills, and a cartilage lying in the fenestra ovalis, but know not what word to substitute, since this cartilage is not the equivalent of the »columella« of the Anura, and is of questionable homology with the »stapes« of higher Vertebrata.

of the cartilaginous capsule bounding the fenestra anteriorly. According to KILLIAN ('90) in *Axolotl*, however, the relations are similar to those in *Necturus*, and the operculum arises quite independently in the neighborhood of the fenestra, but at the side of the cartilaginous ear-case. KILLIAN says that in *Rana esculenta* the fenestra is at first closed by connective tissue in which later the cartilage of the stapedial plate (operculum) arises, and GAUPP ('93) affirms the same for *Rana fusca*. GAUPP describes the operculum, however, as lying in the posterior part of the fenestra ovalis, leaving anteriorly a sickle-shaped space closed only by a membrane. In this anterior space the small cartilage of the pars interna columellae arises. Now in *Triton* and *Siredon* the operculum is described by STÖHR as derived from the anterior wall of the fenestra ovalis, and in *Necturus* the operculum, arising outside the wall of the capsule, lies primarily slightly anterior to the fenestra ovalis. It is consequently possible that the cartilage, called operculum, arising in the membrane closing the oval window of the ear in the *Anura*, is not the homologue of the cartilage called »operculum« in the *Urodela*, which occupies more nearly the position of the pars interna columellae as described by GAUPP.

The primary position of the operculum in *Necturus* is shown in fig. 18, pl. XVIII, a sagittal section through the lateral part of the cartilaginous ear. At the right, in the lower part of the figure, the hyoid cartilage is seen in section, between this cartilage and the fenestra which interrupts the continuity of the otic cartilage, lies a group of cells more compact than the surrounding mesenchyma. In the centre of this group of cells is found the beginning of the operculum. I regret that I am unable to trace the origin of these closely grouped cells. In slightly earlier stages, scattered cells of the mesenchyma occupy the space where in fig. 18 the procartilage cells of the operculum lie.

The cartilage of the operculum is at no time connected with the hyoid cartilage, but this fact does not demonstrate that the cartilage in question may not be a rudimentary element of the hyoid arch, since each element of the cartilaginous arches arises from an independent centre of chondrification, and secondary fusions of cartilaginous elements do not necessarily show original association.

In the embryo of 19 mm, not only has the occipital part of the basal plate fused with the cartilage of the auditory capsule, but the

dorsal extremity of the occipital arch has also united with the inner, posterior, dorsal, corner of the capsule and from the cartilage formed by this union a point reaches dorsalwards towards the Anlage of a cartilage which for a short distance roofs the brain. GAUPP ('93) calls this roofing cartilage *tectum synoticum*, since the name hitherto employed (PARKER '76), *occipitale superius*, belongs properly to a bone, and moreover to a bone not found in the Amphibia. As the relations of this cartilage in *Necturus* make it appear to me desirable that the cartilage be designated by a name which associates it with the occipital arch rather than with the auditory capsule, Prof. GAUPP has suggested that I call the cartilage *interoccipitale*, and I accept the suggestion.

The independent origin of the *interoccipitale* (*tectum synoticum*) is noted by GAUPP ('93), who seems, however, not to have found in the Amphibia which he studied, what is true for *Necturus*, namely, that the cartilage in question is not only independent in origin, but also paired. In *Necturus* 19 mm long, the Anlagen of the *interoccipitale* are still prochondral. STÖHR ('80), who describes the roofing cartilage in *Triton* as connecting the auditory capsules, also demurs at the appellation *occipitale superius*. My reasons for preferring a name which associates the cartilage with the occipital arch are given in the following division of this paper (pages 63, 64).

The procartilage at the base of the first neural arch of the spinal column is primarily separate from the procartilage of the basiscranial plate, but as cartilage begins to form in this arch, the prochondral Anlage at the base of the arch extends forwards and unites with the procartilage of the basal plate in that region, adjoining the chorda and median to the base of the occipital arch, which remains unchondrified at the time when the occipital arch is converted into cartilage. This connecting prochondral tissue has received a special name both from STÖHR and GAUPP, being called by the former, *intervertebro-occipital* tissue, and by the latter *occipito-vertebral* tissue. The tissue in question precedes the formation of a cartilaginous extension from the base of the first neural arch, which grows forwards at the side of the chorda, ultimately appropriating the posterior part of the prochondral tissue that lies between the base of the occipital arch and the chorda.

In the embryo of 19 mm, a complete fusion is found between the cartilage of this anterior extension from the first neural arch

and the occipital cartilage, prior to articulation in the condyles. STÖHR ('80) states that he has not observed in Triton a continuity of cartilage preceding the atlanto-occipital articulation, which would make this articulation resemble that of a spinal arch. GAUPP ('93) also says that he has not observed such a fusion in Rana.

The skull in *Necturus* 46 mm long.

The largest of the small *Necturi* which I raised measured 46 mm, and were eight months old when killed. As the little creatures were raised from the egg in confinement, it is quite probable that the stage of development does not correspond with that of the free animal of the same length. Moreover, the lengths here given are in any case of but relative value, since there is more or less individual variation among animals subjected to the same conditions of environment.

I have made no drawing of a model of this stage, since the changes in the skull are not great and can be easily explained by reference to the model of the skull in the embryo of 19 mm. The chief changes consist in the development of cartilage in connecting bars or plates found as procartilage in the younger embryo, and in the completion of the median wall of the auditory capsule and of the internal partitions which separate the floors of the anterior, posterior, and external semicircular canals from the main auditory chamber.

The branchial cartilages have increased in size, and the procartilage connecting dorsally the bars of the glossopharyngeal and vagus arches in the younger embryo has been converted into cartilage. The trabeculae have become connected by an internasal plate near their anterior extremity, in the region indicated by broken lines in fig. 17. This plate is not an outgrowth from the trabeculae, but arises independently. It underlies the anterior part of the brain, and just beyond its posterior margin the olfactory nerve passes over the trabecula to the nasal epithelium, which is now supported by a narrow band of cartilage, that begins near the external opening of the nose and extends backwards over the dorsal surface of the nasal membrane, ending in a series of fine processes that reach laterally between the folds of the membrane. The nasal cartilage arises independently, as does also the cartilaginous ring that now surrounds the eye. This ring is but three cells wide and one cell deep.

The antorbital processes have chondrified, and a large part of the cartilaginous skull is now incased in bone. The optic and oculomotor nerves pass outwards through two openings in the crista trabeculae as in the younger embryo, and the ramus ophthalmicus profundus trigemini extends forwards between the ascending process of the quadrate and the trabecula, its union with the trigeminal ganglion being roofed by the fusion of the ascending process with the dorsal bar of the crista trabeculae (fig. 16). In the older embryo, however, a cartilaginous process extends backwards from the ascending process and fuses with the anterior wall of the auditory capsule. This process continues the line of the dorsal bar of the crista trabeculae, so that it now appears that the trigeminus, like the opticus and oculomotorius, passes outwards through an opening between the dorsal and ventral bars of the crista. The trigeminal ganglion lies between the quadrate and the auditory capsule, and from the ganglion the mandibular nerve passes outwards external to the ascending process, while the profundus passes forwards median to this process.

With the completion of the median wall of the otic capsule, the large opening found in the younger embryo (fig. 16) has become reduced to four smaller foramina, three of which lie immediately above the floor of the capsule, while the fourth opening is found near the roof of the capsule, vertically above the cartilaginous partition separating the median of the three lower openings from the posterior. The dorsal foramen admits the ductus endolymphaticus. The anterior of the three lower openings admits the facial nerve with the anterior of the two auditory nerves. The median foramen admits the posterior auditory nerve, while the posterior opening is the foramen perilymphaticum.

It is thus seen that in the older embryo a cartilaginous partition separates the two auditory nerves. At the same time a ledge of cartilage which grows inwards from the ventral part of the anterolateral wall of the capsule forms a secondary floor separating the hyomandibular part of the facial ganglion from the auditory chamber. Through an opening left in this inner floor, the anterior auditory nerve, which has entered the posterior wall of the capsule with the facial nerve, passes upwards to the sensory membrane, while the rami hyomandibularis and palatinus pass through the lower and primary floor of the auditory capsule by their respective foramina. As in the younger embryo, the glossopharyngeal and vagus

nerves leave the brain case through a foramen formed by the union of the base and dorsal extremity of the occipital arch with the otic capsule. The opercular cartilage now closes a large part of the fenestra ovalis. The abducens nerve passes through the trigeminal ganglion and onwards with the ramus ophthalmicus profundus. The relations of the facial part of the lateral line system are as in the younger embryo.

A bridge of cartilage now roofs the posterior part of the brain, and is laterally continuous with the cartilage formed by the union of the dorsal extremity of the occipital arch with the postero-dorsal part of the inner wall of the otic capsule. This interoccipital bridge, as previously described, arises independently from paired Anlagen.

In an earlier stage of development the neural arches become connected with one another at their dorsal extremities by a pair of parallel, longitudinal bars of procartilage, which begin to chondrify in continuity with the cartilage of the arches. Before the chondrification is complete, a bridge of procartilage connects the two longitudinal bars between the successive arches. This bridge also chondrifies and the continuous longitudinal bars of cartilage break into pieces that articulate with one another posterior to each transverse bridge. Thus the spinal cord becomes partly roofed, and the articulating processes of the vertebrae are formed.

I believe that in the paired Anlagen of the interoccipitale, we find the equivalent of the longitudinal bars connecting the dorsal extremities of the neural arches of the spinal column, and that the union of these Anlagen to form the interoccipital cartilage corresponds to the transverse union of the longitudinal bars of the trunk. Moreover, it seems that in *Necturus* the interoccipital cartilage actually connects two arches of which the occipital is the posterior.

Figs. 28, 29, and 30 show three sections from an embryo in which as yet but one cartilaginous bridge — that immediately posterior to the facial ganglion — connects the auditory capsule with the basal plate. This bridge is seen in fig. 28, where it is found that the cartilage of the basal plate is directly continuous with the cartilaginous floor of the auditory capsule. The continuity exists but for a few sections, and is almost immediately interrupted at the point *s*. The tissue at the left of this point belongs to the ear, while the cartilage at the right is from the trabecular part of the basal plate. The figure also shows that in the plane of section, the median and dorso-lateral walls of the cartilaginous capsule are

still unformed. The membranous ear, the ductus endolymphaticus, and the auditory ganglion are sectioned.

The plane of fig. 29 passes through the posterior part of the auditory capsule. The cartilaginous floor of the capsule is seen in section at the left, and is found to be no longer connected with the basal plate seen at the right of the figure. A double row of cells however connects the basal plate with a bar of cartilage which lies between the membranous ear and the brain, and which, in later development, becomes part of the postero-median wall of the capsule. The cartilage of the basal plate is here »mesotic«, and the region is that in which the posterior of the two primary connections between the basal plate and the auditory capsule occurs.

A section through the occipital arch is shown in fig. 30. At the left of the figure is seen the vagus ganglion above which muscular tissue from the second myotome is sectioned. Attention need hardly be directed to the striking similarity between the cartilaginous arch seen in fig. 30, and the incomplete arch of fig. 29, or to the manifest difference in the relation of the basal plate to the otic capsule demonstrated by comparison of fig. 29 with fig. 28.

The occipital arch, like the following neural arches, lies primarily in a myoseptum, and in fact in the myoseptum which separates the second myotome from the third (the third postotic somite from the fourth). In the next posterior myoseptum lies the first neural arch of the trunk, and in the plane which separates the first myotome from the second (the second postotic somite from the third) lies that anterior rudimentary arch which is taken into the median wall of the ear. We have therefore in the skull of *Necturus* traces of two cartilaginous arches shown by their relations to the myotomes to be serially homologous with the neural arches of the trunk. The anterior of these arches becomes completely incorporated in the median wall of the auditory capsule, while the posterior, or occipital arch fuses with the auditory capsule dorsally and ventrally, but remains medianly separate, allowing thus the exit of the glossopharyngeal and vagus nerves. The two arches are connected from side to side by an interoccipital cartilage, which, like the cartilage connecting dorsally the neural arches of the trunk, arises from paired Anlagen.

Since that part of the inner wall of the auditory capsule with which the cartilage roofing the posterior part of the brain becomes connected, is derived in *Necturus* from a praeoccipital arch, the appellation tectum interoccipitale seems more adequately descrip-

tive of the roofing cartilage than the topographically accurate tectum synoticum first suggested by GAUPP ('93).

In *Necturus* of 46 mm, the anterior part of the chorda still persists, but lies above the axial cartilage of the basal plate. The chorda enters the plate in the transverse plane passing through the posterior wall of the auditory capsule, and gradually, from the periphery inwards, becomes chondrified, while the tissue bounding the chorda is so modified that the chorda does not come into immediate contact with the cartilage of the basal plate, but passes through the axis of the plate to unite with the anterior prolongation of the first neural arch, thus forming the odontoid process (*Tuberculum interglenoidale* of GAUPP) in the manner described by STÖHR for *Triton*.

A summary of the facts presented in this part of the study is given at the close of the paper.

Part III.

The Muscles.

It is the purpose of the third part of this study to show, chiefly by reference to the figures already described in demonstration of the development of the branchial cartilages, the origin and position of the tissue to which each of the chief muscles of the head, excepting the eye-muscles, may be traced, and further to discuss the segmental relations of the hypoglossus musculature.

I have connected the study of the development of the branchial muscles with that of the cartilages for two reasons; first, because v. KUPFFER ('95, page 119) claims that in *Petromyzon* cells of ectodermic origin similar to those which give rise to the branchial cartilages also take part in the formation of the ventral longitudinal muscle of the branchial region, and secondly because GÖRONOWITSCH ('93, page 254) describes the »periaxiale Stränge«, which are partly composed of neural crest cells, as associated in the bird with the formation of the musculature of the visceral arches.

In *Necturus* the mesectoderm cells do not take part in the formation of muscular tissue, but each muscle of the branchial region may be traced directly to tissue which is from the first distinctly mesodermic. Moreover, NEAL ('97) has recently shown that the muscle thought by v. KUPFFER to be derived in *Petromyzon* from the ectoderm, actually arises by budding from the dorsal myotomes.

MIVART ('69), closely following FISCHER ('64), has given an account of the adult muscles in *Menobranchus* (*Necturus*) which would also serve as descriptive of the muscles in *Necturus* of 46 mm, and I consequently refer to his paper for the final relations and insertions of the muscles, having nothing further to add to the accuracy of his description.

The branchial muscles.

In the embryo of 11 mm, the mesodermic tissues of the head may be divided into three groups, — mesenchymal, mesothelial, and somitic tissues, and it is the mesothelial tissue which gives rise to the branchial muscles. This tissue forms the wall of the pericardium (coelom) and thence extends dorso-laterally or antero-dorsally into each branchial arch. The mesothelium of the mandibular arch is connected with the wall of the pericardium through the mediation of the ventral part of the hyoid mesothelium. In other words, the mandibular and hyoid mesothelia unite with one another ventrally, while the hyoid mesothelium unites with the anterior wall of the pericardium. The pericardial cavity extends into the ventral part of the mesothelium of the hyoid and mandibular arches alone, while in the dorsal part of these arches and in the posterior branchial arches, the body cavity, theoretically present, is completely reduced by the approximation of the cells composing the mesothelial walls.

At its dorsal extremity the mesothelium of the mandibular arch is separate from the mesothelium of the following arches, and passes directly into mesenchyma. The mesothelium of the hyoid arch extends dorsally to the ventral wall of the membranous ear, as shown in fig. 11. Below the posterior wall of the ear, the mesothelium of the hyoid arch is directly continuous with the dorsal part of the mesothelial tissue of the glossopharyngeal arch, as seen from the sagittal section represented in fig. 26, pl. XVIII, where it is also seen that at some little distance above the branchial clefts, the dorsal extremity of the mesothelium of the glossopharyngeal arch is connected in turn by a somewhat broken band of mesothelial tissue with the dorsal part of the united mesothelia of the vagus arches. Thus the mesothelium of the mandibular arch is dorsally independent, while the mesothelial tissue of the following arches is continuous above the gill clefts.

These relations are shown in fig. 26. The plane of section passes vertically through the hyoid mesothelium, but sections only the dorsal

and ventral parts of the mesothelia of the remaining arches. The dotted lines at the right of the figure indicate the union of the ventral part of the mesothelium of the second vagus arch with the dorsal part of the mesothelium of the first vagus arch. The union takes place in sections lateral to the section represented.

In each arch the mesothelial tissue lies in the long axis of a surrounding tube of mesectoderm. The mesectoderm represented in fig. 2, pl. XVI, extends ventrally to the wall of the pericardium from which the mesothelial cords pass dorsalwards through the centre of each mesectodermic arch, sharply distinguished from this tissue by yolk differentiation. As the embryo grows the arc described by each mesothelial cord becomes greater, and the tissue pushes its way from the centre of the arch to the postero-lateral margin, where, on the posterior arches, the buds of the external gills appear. This stage of development is represented in the series, figs. 1 *a*—1 *i*, pl. XVI. The vertical part of the mesothelial cords is seen in section in figs. 1 *a*—1 *c*, while in figures 1 *d*—1 *i*, the union of each successive cord with the wall of the pericardium is represented. Fig. 4, pl. XVI, shows in transverse section, the two-walled mesothelial plate which unites the mesothelial tissue of the hyoid and mandibular arches, seen in horizontal section in figs. 1 *h* and 1 *i*. The anterior part of the mesothelial tissue of the mandibular arch is continuous from side to side in sections that pass below the plane of the section shown in fig. 1 *i*. From this tissue, with little change of relative position the mandibular part of the m. mylo-hyoideus arises, which is innervated by the trigeminal nerve. The hyoid part of the mesothelial plate gives rise to the posterior part of the muscle mylo-hyoideus, which is innervated by the facialis.

In the embryo of 12½ mm, represented in the sections shown in figs. 5 *a*—5 *e*, pl. XVII, the mesothelial tissue of the younger embryo, with very little change of position has been converted into muscular tissue. The muscles of the mandibular and hyoid arches are continuous with the muscular tissue of the mylo-hyoideus, as in the younger embryo the mesothelial tissue of these arches united in the ventral mesothelial plate. In the section shown in fig. 5 *b*, the large mandibular muscle is seen to send a band of muscle fibres to the wall of the branchial chamber. The embryonic muscles appear to come into action before the branchial bars are sufficiently firm to act as levers, and primarily extend from the dense mesectodermal tissue of the arch in which they lie to an adjacent branchial wall.

The first functional activity of the muscle must consequently be exerted by pulling the skin. With the development of cartilage, however, the chief distal attachment is transferred to a neighboring branchial bar.

Fig. 5 *b* also shows an outgrowth from the ventral part of the glossopharyngeal muscle (*glm*) which is not found in connection with the mesothelium of the younger embryo. This outgrowth is the beginning of the muscle cerato-hyoideus internus. In fig. 13, pl. XVIII, a section through the left half of the glossopharyngeal arch is seen, in a plane similar to that of fig. 5 *b*. The figure shows the beginning of the muscle cerato-hyoideus internus in the mesothelial tissue of the glossopharyngeal arch, which is still distinguished by yolk granules. The section is bounded above and at the left by the posterior wall of the hyobranchial cleft. The heart and pericardium are seen in the figure below and at the right. From the wall of the pericardium the mesothelial tissue extends into the glossopharyngeal arch, and the anterior prolongation of this tissue towards the hyobranchial cleft is the beginning of the muscle cerato-hyoideus internus. This muscle is innervated by the glossopharyngeal nerve, and is consequently shown by its innervation as well as by its origin to belong to the third arch. The muscle ultimately connects the cartilaginous bars of the second and third arches.

In fig. 5 *d* a pair of muscles appear which are not derived from the mesothelial tissue of the branchial arches, the muscles genio-hyoidei (*gh*). These muscles form part of the hypoglossus musculature, and their origin will be described later.

In the embryo of 15 mm, represented in figs. 6 *a*—6 *e*, pl. XVII, and 7 *a*—7 *e*, pl. XVIII, the mandibular muscle has nearly lost its connection with the muscle mylo-hyoideus, and has become divided into two parts (figs. 6 *b* and 7 *b*), an external part, the masseter muscle, which extends dorsalwards and ultimately becomes attached to the auditory capsule, and an internal part, the muscle temporalis, which also extends dorsalwards, and ultimately becomes attached to the dorsal wall of the skull. Both muscles are supplied by the trigeminal nerve.

In the embryo of 15 mm, the hyoid muscles have also become distinct. The most dorsal of these muscles lies above the plane of fig. 6 *a*, for the mesothelium of the hyoid arch extends dorsally to the ventral wall of the auditory capsule, as seen in fig. 26, pl. XVIII,

where it is also seen that the dorsal part of the hyoid mesothelium, that part which connects the mesothelium of the hyoid arch with that of the glossopharyngeal arch, forms a distinct mass of tissue, immediately adjoining the more ventral hyoid mesothelium. This dorsal tissue, which lies below the primary centre of chondrification of the auditory capsule, gives rise to the digastric muscle. The muscle retains its primary attachment to the postero-ventral wall of the auditory capsule, but also becomes attached to the dorsal part of the cartilaginous bar of the glossopharyngeal arch, and is ultimately connected with the posterior extremity of the mandibular bar by a long tendon.

The more ventral of the two divisions of the hyoid mesothelium, seen in fig. 26, gives rise to the muscle *cerato-hyoideus externus*, which is widely inserted on the hyoid cartilage, and also becomes attached to the dorsal part of the cartilaginous bar of the glossopharyngeal arch, near the point of attachment of the digastric muscle. Both of these muscles are innervated by the hyoid nerve. The third and most ventral of the hyoid group of muscles is the *mylo-hyoideus*, the origin of which has been described. In fig. 7 *d*, the three hyoid muscles are seen in transverse section (*dig. che. myh.*). In fig. 6 *b*, the *cerato-hyoideus ext.* and the *mylo-hyoideus* are seen in horizontal section.

From the remainder of the dorsal mesothelium seen in fig. 26, the *levator arcuum* arise. That division of this mesothelium which is continuous with the hyoid mesothelium gives rise to the *levator arcus I*, which, with little change of position, becomes connected proximally with the bones investing the posterior auditory region, and distally with the dorsal part of the cartilage of the glossopharyngeal arch. The proximal part of the muscle, however, grows inwards, and ultimately passes beyond the external boundary of the myotomes, which lie in planes median to that shown in fig. 26. The glossopharyngeal nerve innervates this dorsal muscle of the glossopharyngeal arch. From the posterior part of the dorsal mesothelium, seen in fig. 26, the two *levatores* of the vagus arches arise, innervated each by a branch of the vagus nerve.

MIVART ('69, page 456) calls attention to the fact that the levator muscle of the first arch, in the adult *Necturus*, is remarkably distinct from the remaining *levator arcuum*. Fig. 26 shows that even the mesothelium from which the muscle arises is less closely connected with the mesothelium of the vagus arches than with that

of the hyoid. Oddly enough, WILDER ('96, page 295) says that he has sought in vain for the levator arcus I in *Necturus*, and concludes that it is »failing«. The muscle is not small, and is both described and figured by MIVART.

From figs. 5 *a* and 6 *a*, pl. XVII, it is seen that as the stems of the external gills bud out, the small band of muscle, derived from the mesothelium seen in figs. 1 *a*—1 *g* on the postero-lateral wall of each of the three posterior arches, expands into the growing gill bud. Ultimately this muscle band, primarily continuous, breaks into separate parts, and from it also individual muscle cells migrate outwards and find their attachment in the skin. Thus the three systems of gill-tuft muscles arise, dorsally the adductores and levatores branchiarum, and ventrally the depressores branchiarum, supplied by the proper nerve of the arch from which the gill-tuft arises, glossopharyngeal or vagus. The first adductor branchiarum is composed of muscle elements from the glossopharyngeal and first vagus arches which unite above the third gill cleft, and is supplied by a nerve formed from the union of a praetrematic branch of the vagus with a branch of the glossopharyngeus.

There are three constrictores arcuum in *Necturus*. The first grows forwards from the mesothelium of the first vagus arch near the point where this mesothelium joins the wall of the pericardium, in the same manner as the muscle cerato-hyoideus internus grows forwards from the mesothelium of the glossopharyngeal arch. The first constrictor arcuum is supplied by a branch of the vagus nerve which comes through the first vagus arch. The second and third constrictores arcuum arise as a single muscle from the wall of the pericardium in the region where the mesothelium of the second vagus arch unites with the pericardial wall. This muscle is innervated by three branches of the vagus. One from each of the two vagus arches and also by a branch which descends through the trunk posterior to the last branchial cleft, and then turns forwards in the ventral gill region.

The constrictor pharyngis arises from mesothelial tissue posterior to the branchial arches, but similarly related to the walls of the coelom.

We thus find that all of the proper branchial muscles (part of the hypoglossus musculature is secondarily associated with the branchial region) in *Necturus*, may be traced directly to meso-

thelial tissue which is morphologically part of the wall of the coelom. The origin of these muscles from a composite tissue such as the »periaxiale Stränge« which GORONOWITSCH ('92, '93) describes as taking part in the formation of the branchial muscles in the bird, is out of the question.

The hypoglossus musculature.

In the embryo of 15 mm, the somitic divisions of the mesoderm of the head are limited to two somites, which lie respectively lateral to the two vagus roots. Divisions of the axial mesoderm anterior to the first vagus segment have been lost in scattered cells of the mesenchyma which surround the auditory vesicles and bound the walls of the brain, occupying much of the space that separates the neural tube from the external ectoderm.

Although in younger embryos, the mesodermic divisions in the head anterior to the vagus segments are not as distinct in *Necturus* as in the *Selachii*, they nevertheless are constant, and correspond to the divisions determined by v. WIJHE ('82), except that the praemandibular mesoderm is not divided from the mandibular. v. WIJHE tells us regarding the divisions of the mesoderm in the head of the *Selachii*, that the first head-somite, the praemandibular, lies anterior to the mouth. The second head-somite is continued in the mesoderm of the mandibular arch. The third lies above the hyomandibular cleft. The fourth, immediately anterior to the auditory invagination, is widely connected with the mesoderm of the hyoid arch, while the fifth somite, the anterior part of which lies opposite the Anlage of the glossopharyngeal nerve, is connected with the mesoderm of the glossopharyngeal arch. From the sixth somite a myotome arises, and from each of the following somites of the head and trunk myotomes are formed.

Save that there appears to be no early division in *Necturus* between the mesoderm of the praemandibular and mandibular somites, the above description of the divisions of the mesoderm in the *Selachii* is equally applicable to *Necturus* at the time when there are but three branchial clefts. Indications of further divisions of the praecotic mesoderm such as are described by DOHRN ('90) and KILLIAN ('91) in *Torpedo*, or by myself in *Acanthias* ('91), do not appear in *Necturus*. I therefore felt warranted in stating in my first study ('94, page 928) that the segmentation of the mesoderm in *Necturus* is the same as that described by v. WIJHE. To

my surprise both FRORIEP ('94) and SEWERTZOFF ('95) understand me to imply that the head of *Necturus* contains 9 segments. I regret this misunderstanding the more since we read FRORIEP's reviews with no less delight in their clearness, than confidence in their impartial accuracy.

In reviewing my paper on *Acanthias*, FRORIEP ('91 *b*, page 585) also stated, but with better ground for the belief, that I found 12 segments in the head of *Acanthias*. In actual fact, however, I had not studied the occipital region in *Acanthias*, and did not know how many segments enter the head, nor have I at any time made any statement of belief regarding the **number** of segments that enter the head of any Vertebrate. My first study on the segments taken into the occipital region of the head is presented in this paper, and I trust it will appear to those who read the following pages that while I believe it to a certain extent possible to homologize segment with segment in comparing different Vertebrates, I also believe it quite possible that one or more somites have dropped out in the region immediately posterior to the ear, in connection with the reduction of the visceral arches, which would make the number of primitive segments included between the first segment of the head and the last, still undetermined.

Much difference of opinion exists regarding the serial homology of the prae- and postotic divisions of the axial mesoderm. While v. WIJHE believes that the somites he described are serially homologous structures, FRORIEP ('85, '87), not doubting the existence of the nine somites in the Selachian head, maintains that the anterior and posterior somites are not of equal value, and calls attention to the fact that a break exists in the middle of the row, where anterior as well as posterior elements may have been lost. In a brilliant critical review, GEGENBAUR ('87) also expresses his belief that the anterior somites of the head are not homodynamous with the occipital. Welcoming the continuous segmentation described by v. WIJHE as a valuable confirmation of his belief in the segmented structure of the Vertebrate head, GEGENBAUR regards the first 6 of v. WIJHE's somites as belonging to the primitive head, but believes that the 3 posterior somites described by v. WIJHE, have migrated into the head from the trunk. Finally, RABL ('89) takes the extreme view that segmental value can be assigned only to the postotic divisions of the axial mesoderm.

I pause for a moment to comment on a statement by which

RABL ('89, page 228) supports his theory. RABL tells us, »es entwickeln sich bei allen (!) Wirbelthieren die Urwirbel der Reihe nach von vorn nach hinten, so dass also der vorderste Urwirbel zugleich der älteste ist. Dieser vorderste Urwirbel ist aber identisch mit dem fünften (!) Kopfsomit VAN WIJHE's, dem ersten distalen (i. e. postotic) Somite. Auch die weitere Entwicklung der fünf distalen Kopfsomite ist genau dieselbe wie die der nächstfolgenden Urwirbel des Rumpfes (!)«.

Although the chick is a familiar object for the investigation of simple phenomena of development, at the time when I studied ('89) the succession in which the protovertebrae arise, there were, as far as I know, but three published studies describing their order of origin (v. BAER '28—'37, HIS '68, KUPFFER and BENECKE '79), and none of these studies claimed that the most anterior protovertebra is the first to form. I should doubt whether the order in which the protovertebrae arise had been investigated in all Vertebrates, were is not for the authoritative statement of a man (RABL '89, page 115) who warns us that, »der Forscher soll die Wahrheit über Alles halten; er darf sie nie der Klarheit zum Opfer bringen: denn was heute nicht ganz klar ist, kann es morgen werden; aber was heute eine Lüge ist, bleibt in alle Ewigkeit eine Lüge.«

v. WIJHE ('82) says that he believes that the first somites that appear in the Selachii are those of the region corresponding to the neck of higher Vertebrates, and HOFFMANN ('97) confirms this belief, adding that the order of development of the motor nerves, like that of the protovertebrae, is in two directions, thus bringing further evidence against the assumption that successive development in one direction is a prerequisite of homodynamy. KEIBEL ('95) tells us that the first formed protovertebra in the Mammalia is not the most anterior. I also found ('89), and my observation has since been confirmed by GORONOWITSCH ('93), that in the chick, the first division in the axial mesoderm falls between the second and third protovertebrae, and that two protovertebrae are slowly cut off anterior to this primary division of the mesoderm, while the formation of protovertebrae in a posterior direction takes place more rapidly. The protovertebra first formed in the chick is consequently the third in position.

RABL moreover says, as above quoted, that the first protovertebra corresponds to v. WIJHE's fifth somite, and that this protovertebra with the four following (i. e. the five distal head somites) develops

in exactly the same way as the next following protovertebra of the trunk. Now, according to v. WILHE ('82), and both NEAL ('97) and HOFFMANN ('97) confirm the statement, the fifth somite does not develop muscular tissue in the Selachii, being crushed out of existence by the growth of the auditory vesicle, and the muscle-plates begin with the sixth somite, which lies opposite the vagus Anlage.

One is therefore surprised when RABL adds (l. c. page 236), »while foregoing a criticism of the recent hypotheses regarding the metamerism of the Vertebrate head; ich bemerke nur, dass sie mir fast sämmtlich den Eindruck einer Beweisführung um jeden Preis, selbst um den Preis der Thatsachen, gemacht haben«.

It appears to have suited RABL's theory that the muscle-plates should begin with the fifth somite, and should develop from before backwards. Do we, who have other theories, not deserve charitable criticism — even from RABL?

Leaving for the time the question of the metameric value of the segments of the head, I now describe the primitive relations of the postotic divisions of the axial mesoderm in *Necturus*. In fig. 20, pl. XVIII, a sagittal section is shown through the first three postotic somites, corresponding to v. WILHE's 5th, 6th and 7th somites, as indicated by the figures in parentheses. At the right of the section the wall of the alimentary canal is seen, while at the left the section is bounded by ectoderm which deepens anteriorly in the invagination of the auditory epithelium. The Anlagen of three ganglia are sectioned, those of the facial, glossopharyngeal, and vagus nerves. A group of scattered cells partly below the auditory epithelium, partly below the glossopharyngeal ganglion represents the first postotic somite. The mesoderm of the second postotic somite rises higher than that of the first, but is also interrupted by the ganglionic cells above, while the third postotic somite alone reaches the usual height of the protovertebra. It is noticed that the position of the glossopharyngeal and vagus ganglia is such that these ganglia complete dorsally the ventral divisions of the mesoderm above which they lie, giving to the section the semblance of three similar divisions of tissue lying between the endoderm and external ectoderm.

The sections represented in figs. 21 and 22, are from a slightly older embryo than that from which the section seen in fig. 20 is taken, and are reversed in mounting. Fig. 22 shows a section median to that shown in fig. 21. The ganglionic Anlagen are not as large relatively as in fig. 20, since the cells have migrated outwards. In

fig. 21, the first 6 divisions of the postotic mesoderm are seen. The first division lies partly below the auditory vesicle, and partly below the glossopharyngeal ganglion, as in fig. 20. The second division of the postotic mesoderm half surrounds the vagus ganglion, while the third and following divisions are of the usual shape and size. In fig. 22 one sees the first three postotic somites of fig. 21 in a more median plane of section, where the dorsal limit of the posterior part of the first and second postotic somites rises to the plane bounding the dorsal wall of the third and following somites.

Figs. 23 and 24 show sagittal sections from a still older embryo in which the auditory vesicle is nearly separate from the external ectoderm. Fig. 23 shows the more median section. In fig. 24 the first postotic somite, and also the ventral part of the second somite are represented by scattered cells of the mesenchyma. The position of the two somites, however, is easily determined by their relation to the glossopharyngeal and vagus ganglia. The cells of the dorsal part of the second somite are beginning to elongate into muscle fibres, and in the more median section shown in fig. 23, it is seen that these dorsal muscle fibres are continuous with the dorsal part of the third postotic somite. The line separating the two somites is still apparent, but ultimately no segmental division in the band of muscle fibres formed from the dorsal part of the second and third somites is found. Muscle fibres also arise in the group of cells seen in fig. 23 in the postero-ventral part of the second somite. These fibres extend anteriorly and inwards to the lateral surface of the chorda. In horizontal and transverse sections the relations here described are deceptive, and in my second study on *Necturus* ('96, page 506), I mistook the partial fusion of two myotomes for a partial division. I found that the branchial clefts arise intersegmentally, the second or hyobranchial cleft lying beneath the auditory invagination, between the fourth and fifth somites (v. WILHE); the third cleft arises in the plane separating the fifth and sixth, first and second postotic, somites, and the fourth cleft between the second and third postotic somites.

Owing to the fusion of the dorsal parts of the second and third postotic somites, it appeared that when the fifth cleft arose, it also lay between the second and third somites, while the fourth cleft appeared to have migrated forwards and to lie beneath a septum which divided, as I thought secondarily, the ventral part of what seemed to be the second somite. It now appears, however, that

the branchial clefts are from the first strictly intersegmental, and that what seemed a partial division of the vagus somite (second and third postotic), is actually a partial fusion of the two vagus somites. I call these two somites, vagus somites, for the reason that they lie above the vagus arches, respectively external to the two vagus roots.

The anterior part of the neural crest cells of the vagus Anlage extends outwards over the first vagus somite, in the typical manner of cranial nerves, while the posterior part of the vagus Anlage, passes directly downwards, median to the second vagus somite, in the manner of a typical spinal nerve, and becomes attached to the brain in the second vagus root. While the first vagus somite appears to be cut horizontally into dorsal and ventral parts by the anterior vagus nerve, the vagus fibres from the second, posterior, root pass forwards and join those of the main root before passing outwards, so that the second vagus somite remains entire. These relations were noted in my former study, and similar relations have been of late so often noted in other Vertebrates that the separation of cranial from spinal nerves on the ground of their different relations to the axial mesoderm is no longer tenable. The vagus bridges the line of separation and unites the two groups.

The first and second hypoglossus nerves lie median to the fourth and fifth postotic somites. In the plane separating the second postotic somite from the third, lies the rudimentary neural arch, which is taken into the median wall of the auditory capsule (page 64). The first postotic somite does not give rise to muscle fibres, hence the rudimentary neural arch — the praeoccipital arch — lies between the first two myotomes¹. In the myoseptum between the third and fourth postotic somites lies the occipital arch. In each of the following myosepta an arch of the vertebral column is found. The primary relations of the occipital arch to the myotomes appears to me to

¹ I use the word »somite« to designate a primary segmental division of the axial mesoderm. NEAL ('97), following v. WILHE ('82), uses »myotome« as synonymous with »somite«, thus counting with the myotomes, a segmental division of the axial mesoderm, such as the fourth somite of v. WILHE, in which no muscle fibres appear. To my thinking, muscle fibres belong to the making of a »myotome«, and muscle fibres in a primitive relation similar to that of the segmental divisions of the continuous longitudinal muscle of the body. I count the most anterior segment of this longitudinal muscle in *Necturus*, the first myotome, although this myotome arises from the second postotic somite, while in *Petromyzon* (NEAL '97) the first postotic somite also contributes a muscle segment to the longitudinal muscle.

demonstrate that STÖHR ('82) was right in regarding this arch as homodynamous with the neural arches of the trunk.

Having thus acquainted my reader with the early relations of the postotic somites in *Necturus*, before describing the development of the musculature connected with the first two spinal nerves, I pause to compare the postotic divisions of the mesoderm in *Necturus* with those described by SEWERTZOFF ('95) in *Siredon*.

In fig. 27, pl. XVIII, I have copied from SEWERTZOFF's fig. 12, pl. V, a horizontal section through the first postotic somites in *Siredon* at the earliest stage which SEWERTZOFF describes. If this figure (27) be compared with figs. 20, 21, and 22, although the sections are respectively horizontal and sagittal, it will not be found difficult to homologize somite with somite. M_1 the first postotic somite in *Siredon* corresponds with the mesodermic division marked 1 (5) in *Necturus*, and M_2 with 2 (6) etc. I miss, however, from SEWERTZOFF's figure, cells from the glossopharyngeal ganglion. Since the neural crest develops from before backwards, the Anlage of the glossopharyngeus is slightly earlier than that of the vagus, and consequently longitudinal sections passing through the vagus Anlage (fig. 27, *G.n.vg*) must of necessity cut that of the glossopharyngeus also, the cells of which should lie external to M_1 , as the vagus Anlage lies external to M_2 .

In describing these segments, SEWERTZOFF (page 60) says, that the »vordere Segment (M_1) liegt unmittelbar hinter der Gehörblase, sich ein wenig unter dieselbe erstreckend (was man an sagittalen Schnitten dieses Stadiums sieht)«. Again (page 61), »the anterior segment lies vor dem Vagusauswuchs, zwischen ihm und der Gehörblase Der dorsale Theil des vorderen Myotoms fängt bald an zu verkümmern, indem er in zerstreute mesodermale Zellen zerfällt, so dass in den Stadien, wenn die spinalen Wurzeln sich anlegen, seine Reste sich nur an den Seiten der Chorda erhalten Hinter derselben, in der dorsalen Region des Embryos, liegt das zweite Myotom, welches nach außen von der Wurzel des N. vagus liegt«. On page 62, SEWERTZOFF speaks of »das rudimentäre 1-te Myotom, in dessen Fasern ebenfalls eine Querstreifung erschienen ist, seine Reste liegen zwischen der Chorda und der Gehörkapsel der entsprechenden Körperseite«.

Now, according to NEAL ('97), in *Petromyzon* the first postotic somite, occupying the position of M_1 , fig. 27, gives rise to muscle fibres. In the *Selachii*, however, no fibres develop in this somite

(v. WIJHE '82, NEAL '97, HOFFMANN '97) nor does this first postotic segment give rise to muscle fibres in any other Vertebrate above the Selachii of which I know. According to SEWERTZOFF himself, in *Acipenser*, »Die Reihe der Myotome endigt vorn gerade gegenüber dem N. vagus. Nach vorn vom N. vagus habe ich beim Sterlet keine Myotome gesehen« (l. c. page 36).

SEWERTZOFF finds that in *Siredon*, the first ventral spinal nerve lies opposite the third myotome, i. e. the third postotic somite, since the first postotic somite develops muscle fibres. In *Necturus*, the first ventral nerve lies in the fourth postotic segment. In *Siredon*, the occipital arch falls between the second and third postotic segments. In *Necturus*, between the third and fourth. In *Siredon*, the position and fate of the rudimentary muscle developed in M_1 , corresponds to the position and fate of the rudimentary muscle developed in the ventral part of the second postotic somite in *Necturus*. In short, we find that there appears to be one more segment in the head of *Necturus* than in the head of *Siredon*, and that this segment is the first postotic, in which no muscle fibres develop in *Necturus*.

Supposing, however, that we assume that the same fusion between the dorsal parts of the second somite and third takes place in *Siredon* as in *Necturus*, making one apparent segment of the dorsal parts of two, and that in *Siredon*, as in *Necturus*, the ventral part of the second somite becomes separate from the dorsal part, and supposing further that we assume that SEWERTZOFF mistook this ventral part of somite 2 for the rudimentary somite 1, then *Siredon* would correspond with *Necturus*, and it would not appear that a rudimentary muscle arises exceptionally in the first postotic somite, where in no Vertebrate above the Cyclostomata such a muscle is known to appear.

If this assumption be true, as it is certainly plausible, then one segment more than SEWERTZOFF thought enters the head of *Siredon*, and there are, as in *Necturus*, three instead of two occipital segments.

SEWERTZOFF describes the posterior vagus root, and homologizes it with the N. accessorius (l. c. page 64), but failing to distinguish the two vagus segments opposite which the two vagus roots respectively lie, SEWERTZOFF seems not to have recognized their segmental value.

As above mentioned, the ventral part of the second postotic segment gives rise to muscle fibres which are found for some time

at the side of the chorda, adjoining anteriorly the muscle fibres formed in the ventral part of the third postotic somite. As the basal plate develops and the bases of the praeoccipital and occipital arches fuse into its continuous cartilage, the ventral fibres of the second and third postotic somites atrophy, and the ventral fibres of the fourth somite become attached anteriorly to the base of the occipital arch external to the condyles. The muscle formed by the union of the dorsal parts of the second and third somites persists, however, and extends forwards above the auditory capsule. Thus each of the primitive myotomes in *Necturus* is represented in the muscular tissue of the animal 46 mm long, and doubtless of the adult.

Sometime after the union of the dorsal part of the second and third postotic somites, the myoseptum dividing the third postotic somite from the fourth, ceases completely to separate these somites, and it is found that in the median dorsal region, above the spinal column, a pair of long muscle bands extend from the first neural arch, passing the myoseptum between the third and fourth postotic somites without division, to the posterior surface of the muscle temporalis. MIVART says ('69, page 453) that the temporalis muscle »arises from the middle of the upper surface of the skull, and (by fascia) from the first neural spine«. The connection of the temporalis with the first neural spine is accomplished, in *Necturus* of 46 mm, by means of the muscle bands above described, which are composed of fibres from the median dorsal part of the second, third, and fourth postotic somites.

In figs. 23 and 24, two enlargements of the coelom, connected with the development of the pronephros are seen below the fifth and sixth postotic somites, while from the fifth, fourth, third, and possibly from the second somite, strands of cells are seen to extend ventralwards, uniting in a triangular group of mesoderm cells. These cell strands are from buds growing ventralwards from the somites above. Longitudinal sections show the relations indistinctly since the growing buds bend outwards. I have therefore combined the results derived from the study of a number of series of sections in the diagram shown in fig. 25.

At the right of the figure (25), the auditory vesicle is represented, to the left of which, the line of myotomes begins with the second postotic segment. In this segment lies the first vagus root. The muscle fibres of the dorsal part of the second postotic segment are represented as fused with those of the dorsal part of the third

segment, and above the region of fusion the praeoccipital arch is represented. Below the septum which divides the ventral part of the first myotome from the second, lies the fourth visceral cleft. In the third postotic segment is found the posterior vagus root. Along the path marked in fig. 25 by a shaded band, a mesodermic bud grows from the second myotome ventralwards, possibly joined by scattered cells from the first myotome, and bending around the posterior branchial cleft, finally extends forwards and gives rise to the genio-hyoideus muscle, which ultimately finds its anterior attachment on the mandibular arch.

Between the second myotome and the third lies the occipital arch, and below this arch the fifth branchial cleft is found. Since the occipital arch bounds the skull posteriorly, this cleft lies in the region of the head. I mention this fact because SEWERTZOFF ('95, page 71) suggests that the intersegmental position occupied by the branchial clefts in *Necturus* may lead to »der interessanten Thatsache, dass bei *Necturus* nicht alle Kiemenspalten dem Kopfe gehören«.

From the third and fourth myotomes buds also grow ventralwards in close proximity to that from the second myotome. The anterior of these buds gives rise to the muscle sterno-hyoideus. From the diagram it is seen that the paths described by the buds growing ventralwards from the fifth and sixth postotic segments diverge widely from one another in passing around the pronephros, but meet again below the pronephros in the continuous ventral longitudinal muscle of the trunk.

Median to the third myotome lies the first hypoglossus nerve, a dorsal branch from which supplies the musculature developed from the dorsal part of the first and second myotomes. As above mentioned the ventral part of these myotomes atrophies. I have found no dorsal root for either of the hypoglossus nerves, although both nerves possess a ganglion derived in part from cells of the neural crest. FÜRBRINGER ('96, page 487) says that in the *Amphibia* the two first spinal nerves (the hypoglossus nerves) appear, as far as has been observed, to arise as complete nerves with both dorsal and ventral roots. With the second spinal nerve both roots remain throughout life. KINGSBURY ('95, page 149) denies this for *Necturus*, but FÜRBRINGER considers that the denial rests on an individual observation since FÜRBRINGER himself found the dorsal root in the specimen examined.

The spinal ganglia usually lie at the side of the neural cord in early development. The ganglia of the first and second spinal nerves lie in the path of the motor nerve in *Necturus*, at some little distance from the spinal cord. This difference in position signifies perhaps little in itself, except that the space which the dorsal root must traverse in order to reach the spinal cord is considerable, and the root would consequently be less easily overlooked. I suspect, however, that FÜRBRINGER considers a ganglion and a dorsal root equivalent phenomena. The ganglia are there, but I have looked in vain for the dorsal roots of the first and second spinal nerves in *Necturus*.

The ventral branch of the first hypoglossus nerve joins that of the second hypoglossus nerve, and for a short distance the nerves are united, after which the anterior branch extends forwards to supply the genio-hyoideus muscle, giving off branches also to the anterior part of its proper ventral muscle segment, which, in the posterior part, is supplied by the posterior hypoglossus nerve. The third spinal nerve, that of the sixth postotic segment, possesses a large ganglion with a dorsal root, and is the anterior nerve of the brachial plexus.

The slender muscle omo-hyoideus, which secondarily separates from the anterior part of the ventral longitudinal muscle, belongs with the sterno- and genio-hyoideus to the ventral hypoglossus musculature.

On page 82, a table is given, showing the relations of the segmental structures in the occipito-spinal region of *Necturus* in comparison with similar structures found in *Petromyzon* and *Acanthias*. Although the basis of comparison is the serial position of the organs, I would not thereby imply that a somite of *Necturus* is homologous with a somite of *Acanthias* or *Petromyzon*, merely because it occupies the same serial position. On the contrary, I am a believer in the view recently presented in the magnificent study of FÜRBRINGER ('96, page 485), who reminds us, that »since the disappearance of occipital nerves from the head in *Selachii*, *Ganoidei* and *Teleostei* has been amply demonstrated, the postulate that nerves have been lost in the occipital region of the *Amphibia*, where even nerves that come through the free vertebrae degenerate, naturally suggests itself. On the ground that ontogenetic investigation has not as yet actually demonstrated the existence of such nerves, one is to a degree justified in assuming that in the *Amphibia* ontogeny gives a shortened recapitulation of phylogeny, so that these nerves,

Table of the postotic segments in Petromyzon, Acanthias, and Necturus.

Sensory nerves			Somitic nerves			Somites (v. WILHE '82)		Myotomes			Skeletal segments			Visceral clefts ²	
Petromyzon (NEAL '97)	Acanthias (HOFFMANN '94, '97)	Necturus	Petromyzon (NEAL '97)	Acanthias (HOFFMANN '94, '97)	Necturus	Entire Post- otic No.	Petromyzon (NEAL '97)	Acanthias (HOFFMANN '94, NEAL '97)	Necturus	Petromyzon ¹ (SCHNEIDER '79, NEAL '97)	Acanthias (HOFFMANN '94, SEWER- TZOFF '97)	Necturus	Petro- myzon	Nec- turus	
IX IX IX	IX IX IX	IX IX IX	None None None	None None None	None None None	5 5 5	1st 1st 1st	None ³ None ³ None ³	None None None	None None None	None None None	None None None	None None None	None None None	
X ¹ X ¹ X ¹	X ¹ X ¹ X ¹	X ¹ X ¹ X ¹	None None None	None None None	None None None	6 6 6	2nd 2nd 2nd	1st degenerates 1st degenerates 1st degenerates	Dorsal part per- manent. Ventral part degenerates	1st upper vertebral arch	Praeocci- pital arch, rudimentary	Praeocci- pital arch, rudimentary	3rd 3rd 3rd	3rd 3rd 3rd	
X ² X ² X ²	X ² X ² X ²	X ² X ² X ²	None None None	None None None	None None None	7 7 7	3rd 3rd 3rd	2nd 2nd 2nd	2nd 2nd 2nd	2nd 2nd 2nd	Indications of three segments in skull, » Vertebral arches ⁴	Indications of three segments in skull, » Vertebral arches ⁴	4th 4th 4th	4th 4th 4th	
» Vagus 1st occipital enters the vagus (NEAL '97)	1st occipital enters the vagus (NEAL '97)	1st hypo- glossus. Ganglion without dor- sal root	1st 1st 1st	1st 1st 1st	1st 1st 1st	8 8 8	4th 4th 4th	3rd 3rd 3rd	2nd to 4th myotomes give rise by buds to the ventral hypoglossus musculature	2nd upper arch	1st vert. arch	1st vert. arch	5th 5th 5th	5th 5th 5th	
1st spinal 2nd occ. degenerates	2nd occ. degenerates	2nd hypo- glossus. Ganglion without dor- sal root	2nd 2nd 2nd	2nd 2nd 2nd	2nd 2nd 2nd	9 9 9	5th 5th 5th	4th 4th 4th	» 4th 2nd trunk » 2nd 2nd trunk » 5th 3rd trunk	2nd upper arch	2nd v. a.	2nd v. a.	6th 6th 6th	6th 6th 6th	
2nd 3rd occip. Dorsal root degenerates. Ganglion permanent on the 4th occ. somitic nerve	3rd occip. Dorsal root degenerates. Ganglion permanent on the 4th occ. somitic nerve	3rd spinal 3rd spinal 3rd spinal	3rd 3rd 3rd	3rd 3rd 3rd	3rd 3rd 3rd	10 10 10	6th 6th 6th	5th 5th 5th	» 5th 3rd trunk	3rd u. a.	Occipital arch	3rd v. a.	8th 8th 8th	8th 8th 8th	
3rd 1st spinal 4th	1st spinal 4th	4th 4th 4th	4th 4th 4th	4th 4th 4th	4th 4th 4th	11 11 11	7th 7th 7th	6th 6th 6th	» 6th 4th trunk	4th u. a.	1st vert. arch	4th v. a.	9th 9th 9th	9th 9th 9th	
4th 2nd 5th	2nd 5th	5th 5th 5th	5th 5th 5th	5th 5th 5th	5th 5th 5th	12 12 12	8th 8th 8th	7th 7th 7th	» 7th 5th trunk	5th u. a.	2nd vert. arch	5th v. a.	10th 10th 10th	10th 10th 10th	
5th 3rd 6th	3rd 6th	6th 6th 6th	6th 6th 6th	6th 6th 6th	6th 6th 6th	13 13 13	9th 9th 9th	8th 8th 8th	» 8th 6th trunk	6th u. a.	3rd vert. arch	6th v. a.	11th 11th 11th	11th 11th 11th	
6th 4th 7th	4th 7th	7th 7th 7th	7th 7th 7th	7th 7th 7th	7th 7th 7th	14 14 14	10th 10th 10th	9th 9th 9th	» 9th 7th trunk	7th u. a.	4th vert. arch	7th v. a.	12th 12th 12th	12th 12th 12th	
7th 5th 8th	5th 8th	8th 8th 8th	8th 8th 8th	8th 8th 8th	8th 8th 8th	15 15 15	11th 11th 11th	10th 10th 10th	» 10th 8th trunk	8th u. a.	5th vert. arch	8th v. a.	13th 13th 13th	13th 13th 13th	
8th 6th 9th	6th 9th	9th 9th 9th	9th 9th 9th	9th 9th 9th	9th 9th 9th	16 16 16	12th 12th 12th	11th 11th 11th	» 11th 9th trunk	9th u. a.	6th vert. arch	9th v. a.	14th 14th 14th	14th 14th 14th	

¹ The pronephric tubules lie under those myotomes marked by a star. Petromyzon, according to the metamorphism described by HARTSCHKE ('92). I do not accept the conclusions reached by HARTSCHKE, and have consequently combined the myotomic relations given by NEAL ('97), with the skeletal relations given by SCHNEIDER ('79). ² The visceral clefts in the Selachii are not strictly segmental in their relations to the somites, and difference of opinion exists regarding their metameric position. There are 6 clefts in Acanthias. ³ See foot-note, page 76. ⁴ SEWERTZOFF ('95, page 78) shows the segmental position of the upper vertebral arches in

the previous existence of which comparative anatomy renders most probable, do not appear, even passingly, in embryonic development. To me (FÜRBRINGER), it seems that one may draw this conclusion with better right than with SEWERTZOFF assume that the occipital arch which fuses with the palaeocranium in the Amphibia corresponds to the first occipital vertebra of *Acanthias*, while the first three free vertebrae in the Amphibia correspond to the last three occipital arches taken into the skull of this Selachian. SEWERTZOFF hereby assigns the Amphibia a much more primitive position than the Selachii, thus inclining towards the view of STÖHR, against which GEGENBAUR ('87, page 72) has already protested.

However, when FÜRBRINGER adds that to him the so-called occipital arch of the Amphibia, presupposing its phylogenetic reality, seems rather the rudiment of a multiplum of primary occipital vertebrae, I find that the relation of the occipital arch to the myotomes in *Necturus* speaks against such an assumption, but I think that FÜRBRINGER may be right in homologizing the boundary between the skull and vertebral column in the Amphibia with that in the Selachii.

From the comparison of the development of the *m. parietalis ventralis branchialis* in *Petromyzon* with that of the *hypoglossus* musculature in *Acanthias*, NEAL ('97, page 460) infers »that as the branchial basket became reduced in extent, myotomes progressively farther forward grew ventrad to meet in the mid-ventral line«, but calls attention to the fact that while five myotomes take part in the formation of the branchial part of the ventral longitudinal muscle in both forms, the myotome which gives rise to the anterior part of the muscle in *Acanthias* lies three segments anterior to that which gives rise to the corresponding part of the muscle in *Petromyzon*. Thus a difference of three mesomeres is found with a coincident reduction of but two branchiomeres. *Acanthias* has six visceral clefts, and *Petromyzon* eight.

But three myotomes take part in the formation of the *hypoglossus* musculature in *Necturus*, unless the second somite also contributes a few scattered cells, which is doubtful. From the table (page 82) it is seen that the anterior of these three myotomes lies one segment anterior to that which gives rise to the anterior *hypoglossus* bud in *Acanthias*. Since *Necturus* has one branchial arch less than *Acanthias*, this relation of the myotomes to the *hypoglossus* musculature might be regarded as supporting NEAL's view

that the myotomes successively grow ventrad as the reduction of the branchial arches permits them to do so, were it not that the myotome which gives rise to the anterior bud of the hypoglossus musculature in *Necturus* lies above — not posterior to — the second vagus arch (see also fig. 25). As straws show which way the wind blows, this simple fact appears to me to justify FÜRBRINGER's theory regarding the replacement of occipital somites by somites originally belonging to a posterior region. The myotome which gives rise to the anterior part of the ventral hypoglossus musculature in *Necturus* has migrated forwards in phylogeny from its original position posterior to the branchial clefts.

On the evidence furnished by *Amphioxus* and *Bdellostoma* (see PRICE '96) we may surely assume the ancestral Vertebrate to have had a great number of gill clefts, which were by no means confined to the region we now call the head. It is also probable that these gill clefts lay below the myosepta (*Bdellostoma*, *Petromyzon*, *Necturus*) which separated the individual members of the row of axial muscle segments that extended throughout the length of this primitive Vertebrate. With the development of the ear from an integumentary sense organ in this *Amphioxus*-like creature, two axial muscle segments, which correspond in position to v. WIJHE's fourth and fifth somites, appear to have been crushed out of existence. Thus the line of myotomes with their associated nerves and supportive tissue was interrupted, and it seems highly probable that as the branchiomeres became reduced posteriorly, the myotomes with their nerves and supporting tissues slipped forwards and became correspondingly reduced immediately posterior to the auditory vesicle.

If this supposition be correct, each postotic segment of the head is of heterogeneous composition, and the sixth somite of v. WIJHE does not belong primarily to the segment in which it lies, or to the palaeocranium, but like all of the somites posterior to the ear has wandered into a region to which it was primarily foreign. The primitive postotic segments of the head are represented alone by the branchial arches, the glossopharyngeal nerve, and the nerves of the two vagus roots. A corollary is that the number of segments included in the skull between the trabeculae and the last occipital arch is equal to the number of branchial arches possessed by the ancestral vertebrate.

Summary of chief results.

Part I. a) The branchial cartilages and the anterior part of the trabeculae arise in tissue of ectodermic origin.

b) The basal plate of the skull, the auditory capsules, and the occipital arch are of mesodermic origin.

The conclusions reached in Part I are discussed in the Introduction.

Part II. a) The plate of prochondral tissue which primarily underlies the brain is not coextensive with the basal plate of the skull, but includes in its antero-median part prochondral tissue surrounding the point of the chorda, which is not converted into cartilage.

b) Distinctly separate cartilaginous elements, the homologues of the independent trabecular and occipital plates found in Triton, do not appear in Necturus in the development of the basal plate, although a middle region of the prochondral plate chondrifies slightly later than the anterior and posterior regions of the plate.

c) The operculum auris arises near the antero-ventral margin of the fenestra ovalis in cells of the mesenchyma external to the auditory capsule.

d) The dorsal part of the crista trabeculae arises independently, and is possibly the rudiment of the large alisphenoid cartilage found in the Selachii.

e) A rudimentary arch, shown by its relation to the myotomes to be serially homologous with the occipital arch and the neural arches of the trunk, is taken into the otic capsule.

f) The cartilage roofing the posterior part of the brain, tectum interoccipitale, arises independently from paired Anlagen and becomes connected with the dorsal extremities of the occipital and praeoccipital arches, as the cartilage roofing the spinal cord, which also arises from paired Anlagen, is connected with the neural arches.

Part III. a) Each of the proper branchial muscles may be traced to mesothelial tissue primarily continuous with the wall of the pericardium, and is consequently formed morphologically in the wall of the coelom. No branchial muscle in Necturus arises in tissue similar to that composing the »periaxiale Stränge« described by GORONOWITSCH as taking part in the formation of the branchial musculature in the bird.

b) The first postotic somite gives rise to no muscle fibres.

c) The second postotic somite is divided into a dorsal and ventral part by the vagus ganglion. Each part gives rise to muscle fibres. The ventral fibres atrophy, while the dorsal fibres become attached, without myoseptum, to the fibres formed in the dorsal part of the third postotic somite, and are permanent.

d) In the plane separating the second postotic somite from the third, or the first myotome from the second, lies the praeoccipital arch. In the myoseptum between the third and fourth postotic somites, the second and third myotomes, lies the occipital arch. In each following myoseptum, an arch of the vertebral column is found. There are consequently three occipital somites in the head of *Necturus*.

e) Unless SEWERTZOFF mistook, as seems to me probable, the muscle formed in the ventral part of the second somite for a muscle formed in the first somite, there is one more segment in the head of *Necturus* than in *Siredon*, and this segment is the first postotic

f) The first and second vagus roots lie respectively median to the second and third postotic somites. The two hypoglossus nerves lie respectively median to the fourth and fifth somites. The anterior hypoglossus nerve innervates the muscle fibres derived from the second, third, and fourth postotic somites.

g) The ventral hypoglossus musculature arises by buds from the second, third, and fourth myotomes (third, fourth and fifth postotic somites). The second myotome gives rise to the muscle genio-hyoideus. The third myotome gives rise to the muscle sterno-hyoideus.

h) The myotome which gives rise to the muscle genio-hyoideus lies above, not posterior to, the fifth visceral (second vagus) arch, and the bud which forms this muscle consequently grows first posteriorly around the fifth visceral cleft, thus indicating that the somite in question has migrated forwards from a position originally posterior to the branchial arches. The vagus somites should consequently be regarded as elements foreign to the segments in which they lie, and the sixth somite (v. WIJHE) is probably not an integral part of the primitive vertebrate head, to which the branchial arches and the three posterior cranial nerve roots, one glossopharyngeal and two vagus, belong.

i) The second postotic somite in *Necturus* is possibly the homologue of the third postotic somite in *Acanthias*.

j) The branchial clefts are intersegmental in original position.

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Explanation of Abbreviations.

- | | |
|---|--|
| <p><i>ac.</i> cartilage or procartilage of auditory capsule,
 <i>ali.</i> alimentary canal,
 <i>aop</i> antorbital process,
 <i>ar.</i>¹⁻⁴ first to fourth neural arches,
 <i>au.</i> auditory vesicle,
 <i>aud.</i> auditory capsule,
 <i>av.</i> mandibular artery,
 <i>bcp.</i> basicranial plate,
 <i>br.</i> brain,
 <i>br.plx.</i> brachial plexus,
 <i>b'—b'.</i> space enlarged in fig. 1 <i>b'</i>,
 <i>b.</i>¹⁻² first and second basibranchial cartilages,
 <i>cb.</i>¹⁻² first and second cerato-branchial cartilages,
 <i>ch.</i> chorda dorsalis,
 <i>che.</i> m. cerato-hyoideus externus,
 <i>chi.</i> m. cerato-hyoideus internus,
 <i>chy.</i> cerato-hyal cartilage,
 <i>cl.</i>¹⁻⁵ hyomandibular and following branchial clefts,
 <i>con.</i>¹⁻³ first to third m. constrictores arcuum,
 <i>dig.</i> m. digastricus,
 <i>ect.</i> ectoderm,
 <i>end.</i> endoderm,
 <i>epb.</i>¹⁻³ first to third epibranchial cartilages,
 <i>fb.</i> margin of the mesectoderm over which the fore-brain passes,
 <i>fo.</i> fenestra ovalis,
 <i>f.</i>¹⁻⁴ visceral folds,
 <i>f.</i>^{1VII} foramen for ramus hyomandibularis facialis,
 <i>f.</i>^{2VII} foramen for ramus palatinus,
 <i>gh.</i> m. genio-hyoideus,
 <i>gl.</i> glossopharyngeal arch,
 <i>glc.</i> cartilage of glossopharyngeal arch,
 <i>glm.</i> muscle of glossopharyngeal arch,
 <i>glp.</i> procartilage of glossopharyngeal arch,
 <i>G.n.vg.</i> vagus ganglion (SEWERTZOFF),
 <i>g'—g'.</i> space enlarged in fig. 1 <i>g'</i>,
 <i>hh.</i> hypohyal cartilage,
 <i>hmp.</i> hyomandibular pocket,
 <i>hp.</i> procartilage of hyoid arch,
 <i>ht.</i> heart,
 <i>hy.</i> hyoid arch,</p> | <p><i>hybrcl.</i> hyobranchial cleft,
 <i>hyc.</i> cartilage of hyoid arch,
 <i>hym.</i> muscle of hyoid arch,
 <i>hymes.</i> mesothelium of hyoid arch,
 <i>hyp.</i> hypophysis,
 <i>inf.</i> infundibulum,
 <i>i'—i'.</i> space enlarged in fig. 1 <i>i'</i>,
 <i>m.</i> mouth,
 <i>mc.</i> mandibular cartilage,
 <i>md.</i> mandibular arch,
 <i>mdm.</i> muscle of mandibular arch,
 <i>mect.</i> mesectoderm,
 <i>mes.</i> mesothelium,
 <i>Mkp.</i> procartilage of MECKEL'S bar,
 <i>mp.</i> procartilage of mandibular arch,
 <i>myh.</i> m. mylo-hyoideus,
 <i>my'.</i> first myotome (2nd postotic segment),
 <i>m.</i>¹⁻⁴ first to fourth myotomes (SEWERTZOFF),
 <i>n.</i> nasal epithelium,
 <i>na</i>¹. first neural arch,
 <i>occ.</i> occipital cartilage,
 <i>op.</i> oral pocket,
 <i>oph.</i> margin of mesectoderm over which the ramus ophthalmicus profundus trigemini lies,
 <i>opl.</i> operculum auris,
 <i>ops.</i> optic stalk,
 <i>pc.</i> pericardium,
 <i>p.occ.</i> praeoccipital arch,
 <i>prn.</i> pronephric tubules,
 <i>pr.</i>^{1,2} first and second pronephric segments,
 <i>pr.</i>^{1,2c.} enlargements of coelom connected with the two pronephric segments,
 <i>Q.</i> quadrate cartilage,
 <i>Qa.</i> ascending process of the quadrate,
 <i>s.</i> point where the trabecular cartilage unites with the auditory,
 <i>spb.</i> suprapericardial body,
 <i>spn.</i>^{1,2} first and second spinal nerves (hypoglossus),
 <i>spn.</i>³ third spinal nerve (first brachial),
 <i>thy.</i> thyroid outgrowth,
 <i>tr.</i> trabeculae,
 <i>v.</i> blood vessel,
 <i>va.</i>^{1,2} first and second vagus arches,
 <i>vm.</i> ventral longitudinal muscle,</p> |
|---|--|

v.1,2m. muscle of first and second vagus arches,
II. optic nerve,
III. oculomotor nerve,
V. trigeminal ganglion,
VII. facial ganglion,

VIII. auditory ganglion,
IX. glossopharyngeal ganglion,
X. vagus ganglion,
1 (5), 2 (6) etc. postotic segments, the figure in parenthesis gives the number of the head somite (v. WIJHE).

Explanation of Figures.

Plate XVI.

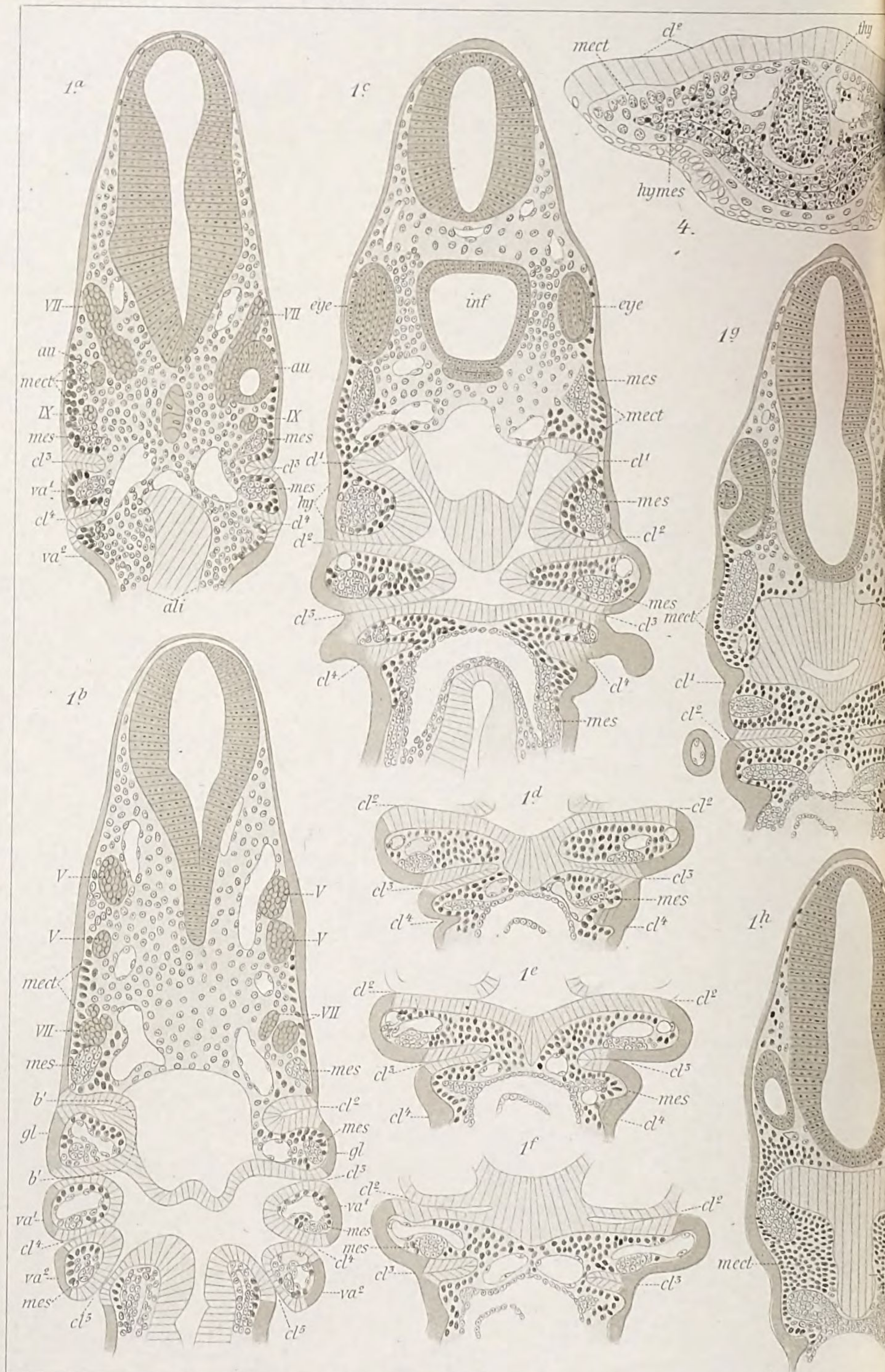
- Fig. 1. Head of an embryo 11 mm long.
 Figs. 1 *a*—1 *i*. Horizontal sections through the head of an embryo 11 mm long.
 Fig. 1 *b'*. Left glossopharyngeal arch from fig. 1 *b*, enlarged.
 Fig. 1 *g'*. Right glossopharyngeal arch from fig. 1 *g*, enlarged.
 Fig. 1 *i'*. Left mandibular arch from fig. 1 *i*, enlarged.
 Fig. 2. Model of the mesectodermic connective tissue in an embryo 10 mm long.
 Fig. 3. Model of the wall of the branchial chamber in an embryo 10 mm long.
 Fig. 4. Transverse section through the thyroid outgrowth.

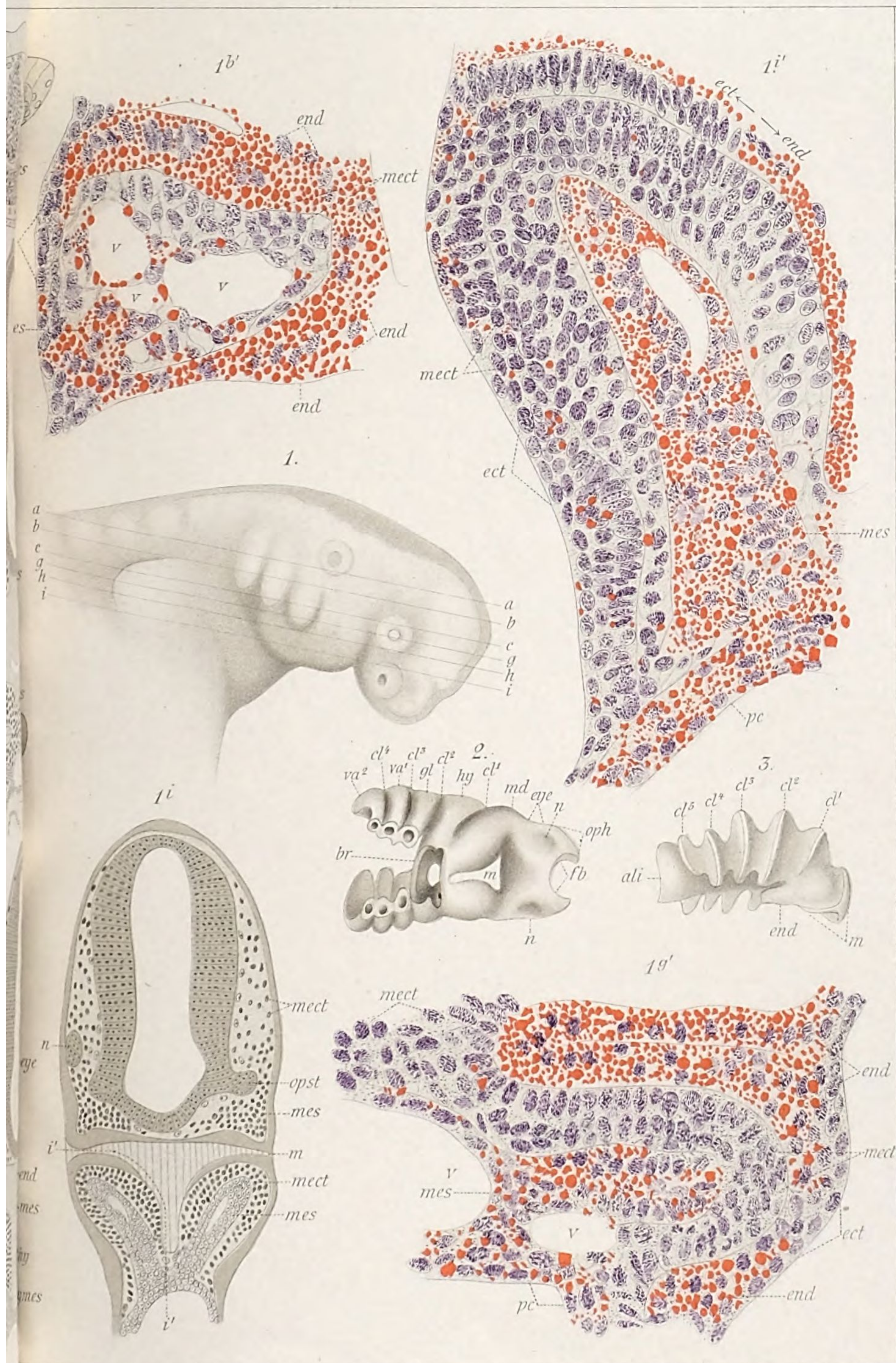
Plate XVII.

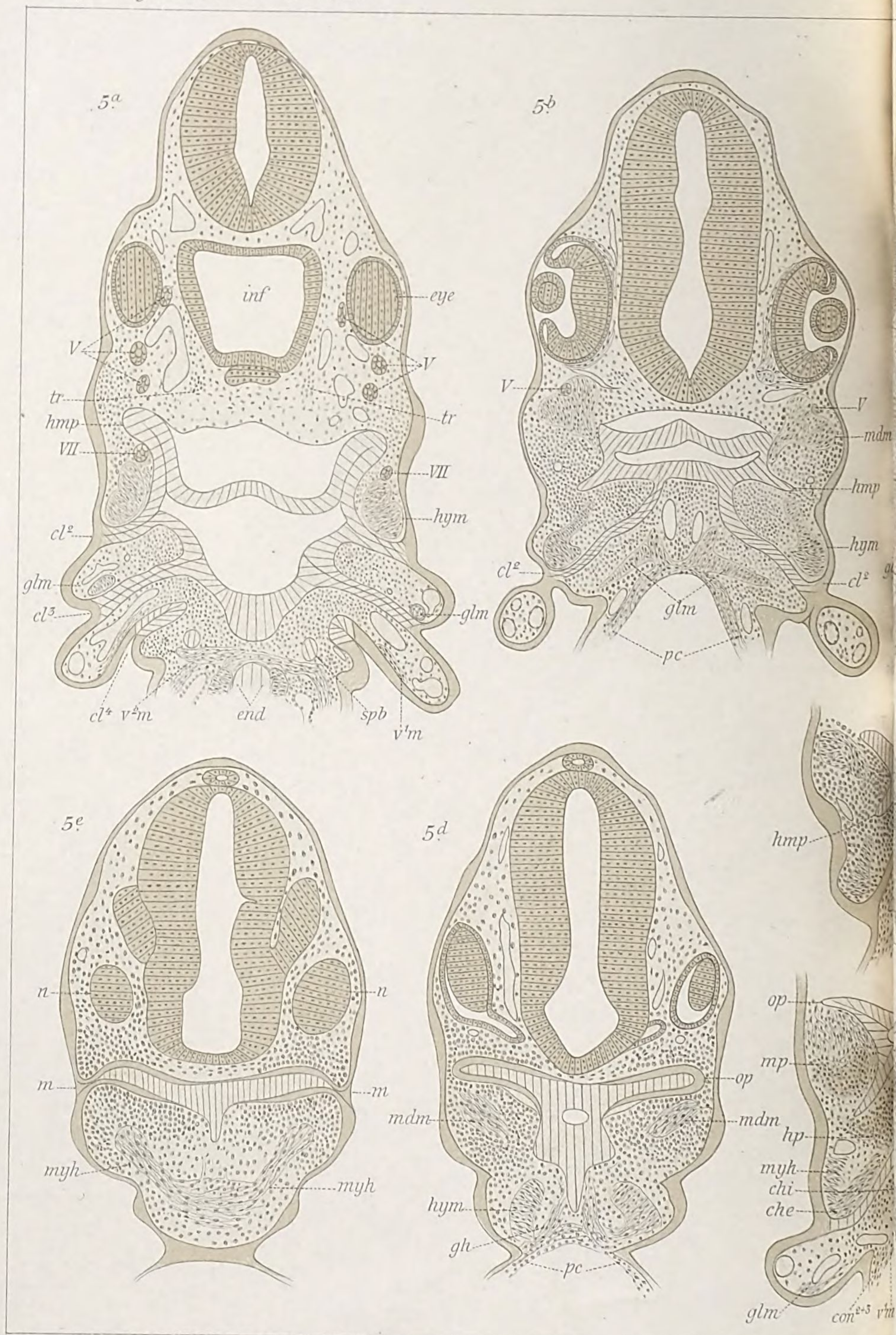
- Figs. 5 *a*—5 *e*. Horizontal sections through the head of an embryo 12½ mm long.
 Figs. 6 *a*—6 *e*. Horizontal sections through the head of an embryo 15 mm long.

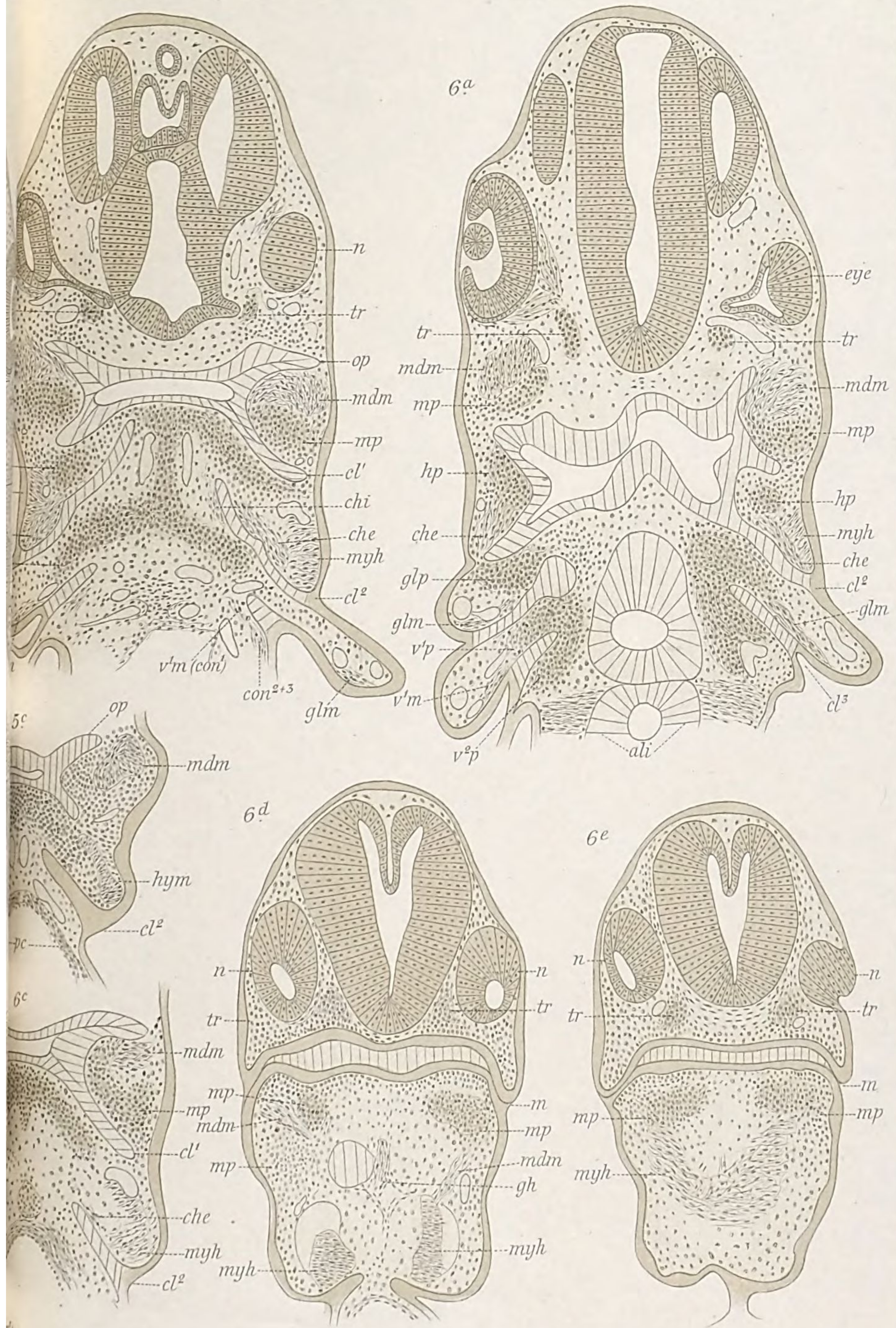
Plate XVIII.

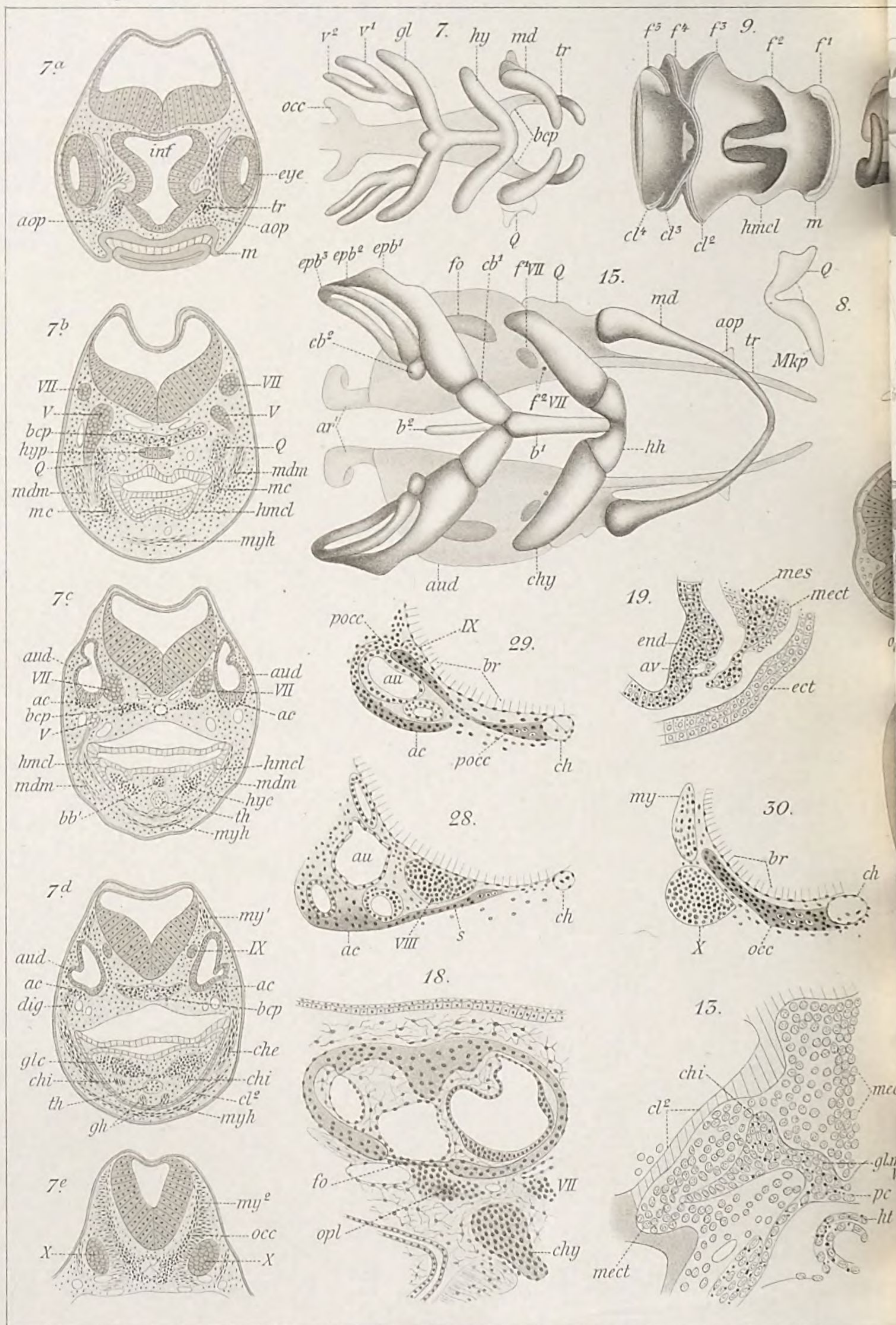
- Fig. 7. Model of the prochondral bars in *Necturus*, 15 mm long.
 Figs. 7 *a*—7 *e*. Transverse sections through the head of *Necturus*, 15 mm long.
 Fig. 8. Procartilage of the mandibular arch.
 Fig. 9. Model of the wall of the branchial chamber in *Necturus* 15 mm long.
 Fig. 10. Sagittal section through the trabecular procartilage.
 Fig. 11. Transverse section through the auditory vesicle, and the dorsal part of the mesothelium of the hyoid arch.
 Fig. 12. Transverse section through the auditory vesicle, and the first procartilage of the auditory capsule.
 Fig. 13. Horizontal section showing the Anlage of the m. cerato-hyoideus internus.
 Fig. 14. Diagram of the basal plate.
 Figs. 15. 16. Model of the cartilaginous skull in *Necturus* 19 mm long.
 Fig. 17. Transverse section through the auditory capsule.
 Fig. 18. Sagittal section through the Anlage of the operculum auris.
 Fig. 19. Transverse section through the mandibular arch and artery.
 Figs. 20—24. Sagittal sections through the postotic segments.
 Fig. 25. Diagram of the postotic segments.
 Fig. 26. Sagittal section showing the mesothelium of the branchial arches.
 Fig. 27. Copy of a horizontal section through the postotic somites in *Siredon pisciformis*, from fig. 12, plate V, SEWERTZOFF '95.
 Fig. 28. Transverse section through the Anlage of the auditory capsule in *Necturus*.
 Fig. 29. Transverse section through the praeoccipital arch.
 Fig. 30. Transverse section through the occipital arch.

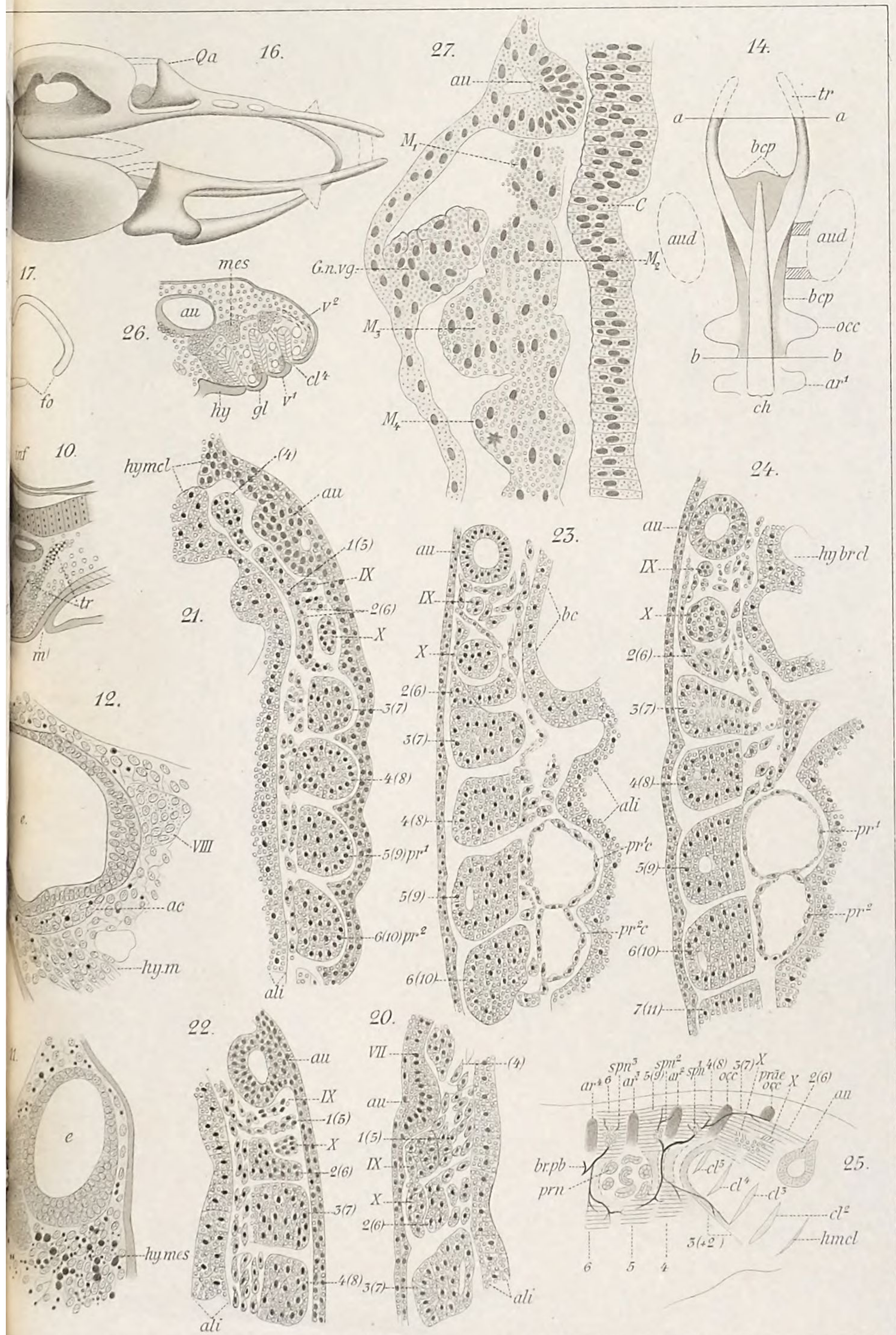












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